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NATURAL HISTORY OF THE SWAINSON'S WARBLER



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NATURAL HISTORY
OF THE
SWAINSON'S WARBLER

by Brooke Meanley, *Wildlife Biologist*

Patuxent Wildlife Research Center

Division of Wildlife Research

BUREAU OF SPORT FISHERIES AND WILDLIFE



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Photographs are by the author unless otherwise credited.



A pair of Swainson's Warblers at their nest near Jacksonville, Fla.
(Photograph by Samuel A. Grimes).

Introduction

The Swainson's Warbler (*Limnothlypis swainsonii*) is one of the least known of songbirds in the southern United States and one that is widely sought by bird enthusiasts. It is unusually appealing to the student of birds because it is hard to find, because its forbidding habitat is challenging, and because it is associated with the Audubon-Bachman period of North American ornithology.

The difficulty of becoming well acquainted with the Swainson's Warbler has been noted by a number of field ornithologists. In the Alabama River bottoms, Arthur H. Howell of the U.S. Biological Survey reported (1928, p. 284-285) it as confined to the deep swamps and riverbottom woods where canebrakes occur, and remarked that its secretive habits conceal it from all but the most persistent observers. In the big swamps above Mobile in May 1911, July 1913, and May 1914 he heard at least nine of these warblers, but because of the impenetrable vegetation was unable to collect any.

Maurice G. Brooks, Professor of Wildlife Management at West Virginia University, and his coworker W. C. Legg (Brooks and Legg, 1942, p. 81) found this elusive warbler extremely difficult to observe in the dense shadows of the "rhododendron hells" of the Alleghenies:

With their neutral brown coloration, their rapid movements, and their apparent liking for the centers of the thickets, they seemed to blend imperceptibly into their surroundings.

While the remarks of Sprunt and Chamberlain (1949, p. 435) are generally true—that "Swainson's Warbler remains today one of the few land birds really difficult to find and study"—there are times when it can be observed at closer range than almost any other songbird. It is not a very suspicious bird. It seems hard to find chiefly because of the character of its habitat.

The bird student seeking this species in a briery-viny entanglement or canebrake disrupts the peaceful atmosphere of the bird's home, naturally frightening it. Or perhaps it is the never-ending wall of nearly impenetrable vegetation between the observer and the bird that discourages one. But in some habitats, when the

birds are on breeding territories, and especially during the courtship and preincubation periods when the pair are traveling together, they can often be approached to within 5 feet and kept under observation at close range for many minutes. Several times during its preincubation period, one paired bird fed within 2 feet of my eyes as I lay prone on the ground. I found canebrakes to be the best habitat for sustained observations: the visual conditions are generally uniform, and the birds tend to stay away from the densest part of the canebrake.

Although the Swainson's Warbler is not as abundant as some of the other southern warblers, in 1968 I knew of at least two areas in which I could find 50 individuals in a single day. One of these was the Great Dismal Swamp in southeastern Virginia; the other was the Ocmulgee River floodplain forest, 3 to 5 miles southeast of Macon, Ga., where I first became acquainted with the Swainson's Warbler (Meanley, 1945, p. 395-401). When stationed at Camp Wheeler near Macon, 1944-46, I began making observations in the extensive riverbottom canebrakes, and I returned to this area for further study in 1963 and each spring thereafter through 1968. During these 24 years the habitat and number of individuals remained virtually unchanged.

When living at Alexandria, La., in 1956 and 1957, I made observations in Bayou Boeuf Swamp, at the edge of that central Louisiana city. In Arkansas in 1967 I obtained information on territorial and nesting behavior in the batture (land between the levee and the river), between the mouth of Bayou Meto and Pendleton Ferry, along the Arkansas River. Mountain habitats near the City of Charleston and in Nicholas County, W. Va., were visited during the spring of 1965 and 1966. In 1966 I began observations in the Great Dismal Swamp, a few miles south of Norfolk, Va. This continues to be my main study area.

METHODS

Habitats in breeding territories were analyzed in several ways. Plant species composition was determined by sampling $\frac{1}{4}$ -acre plots. In canebrake and scrub palmetto (*Sabal minor*) habitats, the density and number of stems were determined by sampling 10-foot-square quadrats.

The light-shading effect of the combined canopy, lower tree, and shrub strata was determined in $\frac{1}{4}$ -acre plots of several tracts. A 2-foot-diameter hoop divided into eight equal sections was held directly overhead, and 20 random readings were made, sighting upward. Readings were taken between 11:30 a.m. and

12:30 p.m. on sunny, windless days. To measure the light intensity, I placed a mirror on the ground in the exact spot where a Swainson's Warbler had been feeding less than 1 minute before, held an exposure meter 1 foot above the mirror with the photo-electric cell upward, and took a reading.

Territory-mapping and transect methods were used in making censuses. Dimensions of territories were determined by spot-mapping males on maps marked off into transects or grids. Studies of territorial behavior were facilitated by color-marking birds of both sexes with celluloid or metal leg bands. Birds were captured with mist nets for marking.

Birds taken on the breeding and wintering grounds were weighed shortly after capture; birds taken during migration were weighed after being held in a freezer for various periods of time.

Measurements are from files in the U.S. National Museum. Time is given as Eastern Standard Time unless otherwise indicated. Bird names used in the text are from the A.O.U. Check-list of North American Birds (1957); plant names are from Fernald (1950) and Radford, Ahles, and Bell (1964); and insect names are from Lutz (1935).

ACKNOWLEDGEMENTS

I am grateful to many persons for their contributions to this project. Anna Gilkeson Meanley, my wife, worked with me on several occasions in the Ocmulgee riverbottom canebrakes and in the Great Dismal Swamp. Linda Hall, Lucille F. Stickel, Nancy C. Coon, Paul A. Stewart, and Van T. Harris reviewed the manuscript. Samuel A. Grimes gave me a copy of his superb photograph of a pair of Swainson's Warblers at their nest, and Frederick C. Schmid made several excellent photographs for me. Oliver H. Hewitt of Cornell University presented me with a photograph of John Abbott, and E. Milby Burton of the Charleston Museum gave me permission to use a photograph of the Reverend John Bachman. The Fogg Art Museum of Harvard University and the Harvard College Library made available a copy of John Abbot's illustration of the Swainson's Warbler. H. L. Stoddard, Sr., and Robert A. Norris of the Tall Timbers Research Station, Tallahassee, Fla., gave me specimens that struck the TV tower at the station. Eugene P. Odum and William Dopson of the University of Georgia and James B. Cope of Earlham College gave me data from specimens in their collections. J. Fred Denton of Augusta, Ga., and M. G. Vaiden of Rosedale, Miss., provided me with important data from their studies. John W. Aldrich, Gorman M.

Bond, and Allen J. Duvall of the U.S. Fish and Wildlife Service helped with taxonomic problems and other matters. I also wish to thank Olin Sewall Pettingill, editor of the *Living Bird*, and George A. Hall, editor of the *Wilson Bulletin*, for permitting me to quote extensively from papers of mine appearing in those journals.

History

The Swainson's Warbler was described by Audubon from specimens collected by John Bachman (fig. 1) on the banks of the Edisto River in South Carolina in 1832 or 1833. Audubon named

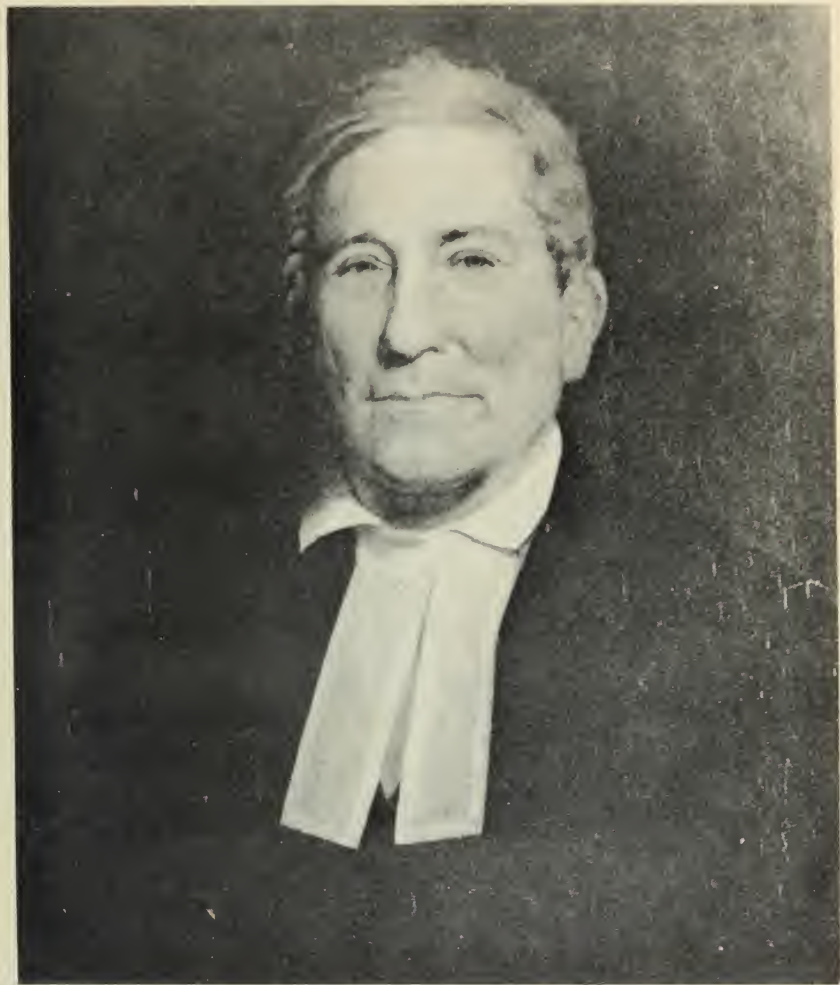


FIGURE 1.—The Reverend John Bachman. He collected the type specimen of the Swainson's Warbler along the banks of the Edisto River in South Carolina in 1832 or 1833. Photograph courtesy Charleston (S.C.) Museum.



FIGURE. 2.—Audubon's painting of the Swainson's Warbler, from Bachman's type specimen.

the new bird for his friend the English ornithologist William Swainson, giving it the scientific name *Sylvia Swainsonii*.¹ Audubon's painting of the new warbler (fig. 2) appeared in his *Birds of America* (1834a, plate 198). The description appeared in his

¹ The present generic name, *Limnothlypis*, meaning marsh finch, is credited to Stone (1914, p. 26).



FIGURE 3.—The arrow-designated circle in South Carolina marks Bachman's type locality; that in Georgia marks the approximate locality where Abbot collected specimens some 25 years before Bachman.

Ornithological Biography (Audubon, 1834b, p. 564–565). The type specimen was given to the U.S. National Museum by Spencer F. Baird, one-time Secretary of the Smithsonian Institution, who acquired it from Audubon.

The discovery of this new species by Bachman, some 25 miles south of Charleston, is described as follows (in Audubon 1834b, p. 564) :

I was first attracted by the novelty of its notes, four or five in number, repeated at intervals of five or six minutes apart. These notes were loud, clear, and more like a whistle than a song. They resembled the sounds of some extraordinary ventriloquist in such a degree, that I supposed the bird much farther from me than it really was; for after some trouble caused by these fictitious notes, I perceived it near me and soon shot it.

Bachman collected five specimens in the spring of 1832 or 1833. The type locality apparently is in the vicinity of Jacksonboro and Parker's Ferry Landing, S.C. (figs. 3 and 4). Audubon reported



FIGURE 4.—The Edisto River near Jacksonboro in South Carolina, where Bachman collected the type specimen of the Swainson's Warbler.

that the type specimen was collected in 1832, the year that he was on an expedition to Labrador. However, Arthur T. Wayne (1906, p. 227), Charleston ornithologist of the late 1800's and early 1900's, pointed out that since Audubon was in Labrador in 1833 and not 1832 the type specimen must have been collected in 1833.

While John Bachman gets the credit for the discovery of the Swainson's Warbler, John Abbot (fig. 5), a Georgia naturalist, apparently collected a specimen some 25 years earlier but made no public record of the event. However, he made an identifiable portrait of the bird (fig. 6). Many of Abbot's Georgia bird paintings were deposited in the British Museum and the Boston Society of Natural History. Those, including the Swainson's Warbler, deposited in the latter place now repose in the Fogg Art Museum, Harvard University. Walter Faxon (1896, p. 207), one of the first persons to study Abbot's paintings, made the following remarks about the painting of the Swainson's Warbler:

On looking through the Abbot bird-portraits several arrest the eye from their historic interest. Plate 68 is a good representation of Swainson's War-

bler, drawn at least a quarter of a century before this species was described and named by Audubon. On the reverse of the plate is the following autograph note by Abbot: L. 6. May 8. Swamp.—Swamp Worm-eater.



FIGURE 5.—John Abbot (self portrait), Georgia naturalist who collected a specimen of the Swainson's Warbler about 25 years earlier than Bachman, but did not report it. His painting of the bird was discovered many years later. Photograph courtesy Oliver H. Hewitt, Cornell University.

During his first years in Georgia after the Revolutionary War, Abbot lived in the town of Jacksonboro in Screven County. Jacksonboro, no longer in existence, was located in the Savannah River valley near Sylvania. Abbot did much of his collecting in a swamp along Brier Creek (fig. 7), a tributary of the Savannah.



FIGURE 6.—Photograph of John Abbot's painting of the Swainson's Warbler, which he called the "Swamp Worm-eater." Illustration courtesy Fogg Art Museum, Harvard University, and the Harvard College Library.

After Bachman collected his historic five specimens in 1832 or 1833, the Swainson's Warbler was almost a lost species for the next 50 years. According to William Brewster (1885a, p. 66), only eight or nine specimens were collected during that period. Then in 1884, Brewster and Arthur T. Wayne made significant collections and studies in the vicinity of Charleston, S.C. (Brewster, 1885a). Wayne reported the first nest and eggs known to

science (Brewster 1885b, p. 468), near Charleston on June 6, 1885. Troup D. Perry (1886, p. 188) of Savannah, Ga., found a nest 22 days earlier (May 16) but did not report his discovery as soon as did Wayne.

Since the Swainson's Warbler was thought to be restricted to the Coastal Plain, ornithologists were surprised to learn by the 1930's that this warbler was a locally common breeding bird to an elevation of about 3,000 feet in the Southern Appalachians. Before the 1930's there had been several records from the Piedmont suggesting the possibility of an up-country population. L. M. Loomis (1887, p. 347-348) found the bird at Chester, S.C., 150 miles from the coast, and W. H. LaPrade, Jr., (1922, p. 88-89) found a nest with eggs at Atlanta, Ga., 1,050 feet above sea level in the foothills of the Appalachians.



FIGURE 7.—Approximate location on Brier Creek, Screven County, Ga., where Abbot collected the "Swamp Worm-eater."

The first record of this species in the Appalachians is apparently based on a specimen collected on June 14, 1924, by P. C. Bibbee (see Brooks and Legg, 1942, p. 76) in West Virginia. The bird was taken at Buzzard's Rocks, Monongalia County, in what Brooks and Legg describe as "a rugged region of hemlock-and-rhododendron-clad mountains only a few miles from the Pennsylvania border."

Additional early records from the Appalachians are those of T. D. Burleigh, who collected three specimens near Asheville, N.C., on September 17, 1930, August 31, 1931, and September 14, 1932. (in U.S. National Museum collection) and those of E. A. Williams (1935, p. 458-459) who sighted several birds near Tryon, N.C., on May 8, 1934. The Swainson's Warbler was established as a breeding bird of the Appalachians in the summer of 1932 when F. M. Jones discovered several nests in southwestern Virginia near Bristol (Murray, 1939, p. 9).

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Distribution

BREEDING RANGE

The Swainson's Warbler spends nearly 6 months of the year in the United States (fig. 8). During this period the bird is primarily associated with the river floodplain forests and swamps of the South Atlantic and Gulf Coastal Plains, and with the rich moist woods of the Mixed Mesophytic forest (see Braun, 1950, p. 39-49) of the Southern Appalachians. The mountain habitats are in the hemlock-rhododendron (*Tsuga canadensis*-*Rhododendron maximum*) association and the cove hardwoods forest. Apparently the Piedmont Province is generally unsuitable for occupation by this species. While there are scattered records of its occurrence in the Piedmont Province during the breeding season, there appear to be no breeding concentrations in this in-between area. The swamps and floodplain forests of the Coastal Plain, and sections of the Mixed Mesophytic forest where this species occurs in the mountains, are more humid than most of the forests of the Piedmont.

During the summer the climatic features of the two major physiographic regions occupied by the Swainson's Warbler are somewhat similar. Blair (1942, p. 130, 132) has classified the climate of the South Atlantic and Gulf Coastal Plains as Humid Subtropical type, and the climate of the Southern Appalachians as Humid Continental type (warm long summer subtype). The Humid Subtropical climatic type has a moderate-to-heavy rainfall at all seasons, usually with a maximum in summer; 9 to 12 months with mean temperature above 50° F.; and a growing season of 220 days or more. The Humid Continental type (warm long summer subtype) has a rainfall between 20 and 40 inches with a summer maximum; 6 to 9 months with mean temperature above 50° F.; and a growing season of 140 to 220 days.

Atlantic Coastal Plain

Along the Atlantic Coastal Plain the Swainson's Warbler occurs from extreme southern Delaware to southeastern Virginia and southward and inland as far as the fall line to about Jacksonville and the Suwannee River in Florida.

The northern limit on the Atlantic coast is the Pocomoke River Swamp in Sussex County, Del., and Worcester County, Md. The Pocomoke Swamp lies about 10 miles inland from the Atlantic



FIGURE 8.—Distribution of the Swainson's Warbler. Hatched area indicates general limits of breeding range; solid black area indicates general limits of winter range.

Ocean and extends from just above the Delaware-Maryland line southward nearly to the Virginia boundary. Only a few scattered pairs nest in this cypress-gum disjunct swamp.

The Swainson's Warbler is locally common in the Great Dismal Swamp in southeastern Virginia and northeastern North Carolina, and in certain floodplain forests just below the fall line. In many of these river floodplains its distribution coincides with that of the giant cane (*Arundinaria gigantea*). It was also reported to be common in the 1960's in the Ocmulgee River floodplain forest, 3 to 5 miles south of Macon, Bibb County, Ga.; in the Savannah River Valley, from Augusta, Richmond County, Ga., downstream about 25 miles; and in the Wateree River Swamp, northwest Sumter County, S.C. Scattered pairs and singing males have been reported from many other areas in the Carolinas and Georgia.

The distributional status of the Swainson's Warbler in the lower Coastal Plain of South Carolina and Georgia has apparently changed in the last 50 years. In the *Living Bird*, Fifth Annual, (Meanley, 1966, p. 152), I made the following comments regarding the former abundance of this species in the lower Coastal Plain of the Southeast:

At the close of the 19th century and the beginning of the 20th, Swainson's Warblers were apparently more numerous in the lower Coastal Plain than they are today. Wayne (1910:149-150) found them to be common breeding birds near Charleston, South Carolina, as did Perry (1887:142) near Savannah, Georgia. During the period of 22 April to 25 September 1884, Wayne collected 47 specimens of this species near Charleston. Considering modes of travel available to Wayne and the limited area of his operations, his collecting of so many specimens would seem to indicate a sizable population in the area. Perry (1887) reported 24 active nests near Savannah in the spring of 1887, which likewise suggests that Swainson's Warblers were more abundant in the late 19th century than at present. E. S. Dingle of Huger, South Carolina, who worked with Wayne and who bridged the gap between Wayne's time and the present, informed me in April 1958 that he had noted during his lifetime a marked downward trend of the population in the coastal area. A. Sprunt, Jr. (in Sprunt and Chamberlain, 1949:435), a protégé of Wayne's, has seen this warbler only four times in the lower Coastal Plain of South Carolina.

In the lower Savannah River Valley, an area extending 30 miles upriver from Savannah, E. O. Mellinger and I found only scattered individuals and occasional pairs during the early 1960's—certainly not the numbers and concentrations found farther up the valley near Augusta, as reported by Murphey (1937:42), Norris (1963:47), and J. F. Denton (pers. commun.).

Gulf Coastal Plain

In the Gulf Coastal Plain the Swainson's Warbler occurs from north of the Suwannee River in northern Florida, northward and

westward to southern Alabama, eastern, Mississippi, and the lower Mississippi Valley as far as southern Illinois, and westward through southern Arkansas and the southeastern corner of Oklahoma to at least Brazos County, Tex.

During the mid-20th century, areas where it was reported as locally common were mostly in the lower Mississippi Valley. However, the lower Mississippi Valley was the center of the most intensive ornithological investigations during the period. It undoubtedly was common also in many areas east of the lower Mississippi Valley.

In northwestern Florida it was formerly reported as a locally common breeding bird along the Wacissa River near Waukeenah, along the Suwannee River near Old Town (Wayne, 1893, p. 338; 1895, p. 367), and along the Aucilla River (Howell, 1932, p. 386). F. M. Weston (1965, p. 105) regarded it as an uncommon summer resident at Pensacola.

In Alabama it is rather widely distributed, with breeding concentrations in the Alabama River bottoms above Mobile and in the vicinity of Bear Swamp a few miles west of Montgomery (Howell, 1928, p. 284; Imhof, 1962, p. 439).

In the Louisiana section of the lower Mississippi Valley, G. H. Lowery (personal communication, 1962) reported it as commonly breeding in the vicinity of Baton Rouge, and I found it locally common in 1956-57 in Bayou Boeuf Swamp near Alexandria as well as in the Tensas River area a few miles south of Tallulah.

In the Mississippi River Delta, at Rosedale, Bolivar County, Miss., M. G. Vaiden (personal communication, 1968) found nests and reported the species as fairly common in the batture along the Mississippi River.

In eastern Arkansas I found it locally common in the lower White River bottoms, in the East Moon Lake and Scrubgrass Bayou areas, and along the Arkansas River between the mouth of Bayou Meto and Pendleton Ferry. Five nests were located in the latter locality between 1966 and 1968.

Apparently the Swainson's Warbler was a breeding bird in the late 1800's and early 1900's in the St. Francis River "sunken lands" of southeastern Missouri and northeastern Arkansas, where it occurred in canebrakes with the Bachman's Warbler (*Vermivora bachmanii*) (Widmann, 1895, p. 115-117). Since the time of Widmann's investigations, much of the swampland in that area has been drained and the canebrakes destroyed.

At Memphis, Tenn., B. B. Coffey, Jr., (1941, p. 30-31) reported Swainson's Warblers nesting within the city limits and in at least

10 localities in surrounding Shelby County. These warblers occur regularly in most of the Coastal Plain riverbottoms of western Tennessee and in the Reelfoot Lake area. Mengel (1965, p. 389) reported the species as "fairly common locally in lowland forests of extreme western Kentucky (Fulton, Hickman, and Ballard Counties), rare and local in swamp forests of the Pennyroyal and Western Highlands."

The Gulf Coastal Plain extends as far northward as the southern tip of Illinois, a short distance above the confluence of the Ohio and Mississippi Rivers. Records from the Coastal Plain of southern Illinois are as follows: Olive Branch, Alexander County, May 15 and 20, 1909, and Reevesville, Johnson County, June 21-22, 1909 (Howell, 1910, p. 216); Cairo, Alexander County, September 1, 1938, female collected (Ammann, 1939, p. 185-186); and DuQuoin, Perry County, a few miles north of the Coastal Plain, June 7, 1907 (Gross, 1908, p. 225).

The breeding range of the Swainson's Warbler west of the Mississippi Valley is imperfectly known. It has been found during the breeding season as far west as Brazos County, Tex. (Purrrington, 1966, p. 35); and in southeastern Oklahoma (McCurtain County) just beyond the Coastal Plain (Sutton, 1967, p. 491).

Southern Appalachians

The Swainson's Warbler breeds in the mountains in south-central West Virginia, perhaps southeastern Ohio, eastern Kentucky, southwestern Virginia, eastern Tennessee, western North and South Carolina, and northern Georgia and Alabama.

In West Virginia, Swainson's Warblers occur mostly on the Allegheny Plateau, west of the main Allegheny ridges. M. G. Brooks and W. C. Legg (1942, p. 78) found the species locally common near Mt. Lookout, Nicholas County, where elevations are between 2,200 feet and 1,300 feet at the Gauley River level. The three principal streams along which Swainson's Warblers were found are Gauley River; Collison Creek, a tributary of the Gauley; and Anglins Creek, a tributary of Meadow River.

The Swainson's Warbler breeds commonly in the mountain ravines opposite Charleston, W. Va., in the Kanawha River Valley. Charleston lies at an elevation of about 600 feet, and the birds are found from the city limits upward. Fifty miles west of Charleston, in the Ohio River Valley, there are records from Huntington, W. Va., (Seeber and Edeburn, 1952) and across the river at Chesapeake, Lawrence County, Ohio (Green, 1947, p. 211). M. G. Brooks (1965, p. 281) states that Swainson's Warblers are known from 14 West Virginia counties.

In the mountains of eastern Kentucky this warbler was first noted by G. H. Brieding (1944, p. 6-7) on Black Mountain, Harlan County, on July 5 and 6, 1944. R. M. Mengel (1965, p. 391) collected a specimen on June 26, 1951, near Elkhorn City, on the line between Dickinson County, Va., and Pike County, Ky. The elevation at this point is about 2,200 feet.

Farther south along the Appalachian chain in the Holston Mountains of southwestern Virginia and northeastern Tennessee, nesting has been recorded by F. M. Jones near Bristol, Washington County, Va. (Murray, 1939, p. 9). Three miles northeast of Shady Valley, Johnson County, Tenn., W. M. Perrygo and C. Lingebach collected an adult male at an elevation of 3,000 feet on June 8, 1937, and observed two others at 2,600 feet elevation 5 miles north of Shady Valley near Beaverdam Creek (specimen in U.S. National Museum).

In western North Carolina, T. D. Burleigh collected three specimens near Asheville, in the Pisgah National Forest, one each on September 17, 1930, August 31, 1931, and September 14, 1932 (specimens in U.S. National Museum). At Tryon, near the North Carolina-South Carolina border, E. A. Williams (1935, p. 458-459) observed a Swainson's Warbler on May 8, 1934, and the following year observed a pair from May 9 to 14.

An important concentration area of this species in the Southern Appalachians is where the States of North Carolina, South Carolina, and Georgia meet. H. M. Stevenson, Jr., (1941, p. 46) reported Swainson's Warblers from Highlands, Macon County, N.C., June 20, 1937, at 3,800 feet elevation, and July 3, 1937, at 3,700 feet elevation. J. F. Parnell and T. L. Quay (1964, p. 144) reported Swainson's Warbler "as a rather common summer resident" at Toxaway River Gorge, Transylvania County, N.C. In that area at an elevation of 1,400 feet Parnell observed an adult feeding young. R. H. Peake, Jr., (1965, p. 114) reported finding a bird near Cashiers, Jackson County, N.C., April 22, 1965.

In western South Carolina an adult male was taken by W. M. Perrygo at Walhalla, Oconee County, June 25, 1940. Also in Oconee County, J. B. Shuler (1962, p. 75-76) noted a singing male in the Sumter National Forest, May 19 and 30, 1962.

The first record in the mountains of Georgia was obtained June 3, 1948, by C. Neal and J. F. Denton (Denton, 1948, p. 24-25), at an elevation of 1,700 feet on Tray Mountain near Robertstown, White County. In the same locality, Denton and Neal (1951, p. 27-28) saw three males on May 8, 1949, and four males on May 9, 1950. At Clayton, Rabun County, Ga., E. O. Mellinger (personal

communication) observed two pairs almost daily during April, May, and June 1968.

In Alabama, T. A. Imhof (1962, p. 439) recorded this species in the northeastern corner of the State (Long Island Gulf, Jackson County), at 1,150 feet, June 7, 1957.

Ozark Mountains

There are records of birds in two locations in the Arkansas Ozarks. D. A. and F. C. James and S. Hilty (1966, p. 577) recorded three territorial males 12 miles southeast of Yellville, Marion County, Ark., June 25, 1966. At Fayetteville, Washington County, in the northwestern corner of the State, the Jameses (1966, p. 518) observed a male on territory daily, May 4 to 31, 1966.

Westward beyond the Ozarks, the breeding range extends into the Prairie Plains physiographic region of northeastern Oklahoma. Nice (1931, p. 155) reported that A. J. Kirn located several nests along the Little Caney River near Copan, Washington County, in June 1914 and June 1917. This locality is only about 10 miles from the Kansas border. A more recent occurrence in the same county was reported at Bartlesville, April 23, by S. Veal (Williams, 1966, p. 524).

Piedmont province

The following are records made during the breeding season. Records from the Piedmont province before May and after July may represent either birds on their breeding grounds or migrants.

Virginia.—Charlottesville, in the upper Piedmont, in the foothills of the Blue Ridge Mountains: Summer 1913 (Ferneyhough, 1914, p. 291), and spring 1961 through 1964, by R. S. Merkel (Scott and Cutler, 1964, p. 442).

South Carolina.—Greenwood County, near the Savannah River Valley, approximately 40 miles above the fall line: July 3, 1924, nest (F. W. Hahn in Sprunt and Chamberlain, 1949, p. 436).

Georgia.—Atlanta, in the foothills at an elevation of about 1,200 feet: May 27, 1920, and May 30, 1922, nests (LaPrade, 1922, p. 88-89). Athens: May 20, 1921 (Burleigh, 1938, p. 24).

Kentucky.—Bullitt County: June 27, 1937 (Carpenter, 1937, p. 32).

Extralimital records (United States)

Records of occurrence beyond the limits of the normal breeding range are as follows: Kearney, Neb., April 9, 1905, by C. A. Black (Worthen, 1906, p. 227); Holly, Prowers County, Colo., May 12, 1913 (Lincoln, 1918, p. 236); Prospect Park, New York City,

May 5, 1950, by Carleton and Helmuth (Bull, 1964, p. 362) ; Mt. Carmel, Wabash County, Ill., April 1878 (Ridgway, 1878, p. 163) ; Lake Quivira, Johnson County, Kans., May 11, 1957 (Hardy, 1957, p. 10) ; and Linwood, N.J., May 23, 1968 (Savell, 1968, p. 159).

WINTER RANGE

The main wintering grounds are the Caribbean archipelago in the general area of latitude 20° N., including Jamaica and Cuba, and the Yucatan Peninsula south to British Honduras (fig. 8).²

Cuba

Oriente Province.—Guantanamo: January 18, 1914, male collected (Ramsden, 1914, p. 253).

Las Villas Province.—Cienfuegos: December 23, 1948, through January 3, 1949, several specimens collected (Eaton, 1953, p. 169).

La Habana Province.—Havana: September 25, year ?, one specimen collected, and April 14, 1922, one specimen collected, both possibly migrants (from the distribution files of the Migratory Bird Populations Station of the Bureau of Sport Fisheries and Wildlife, at Laurel, Md.).

Jamaica

St. Thomas Parish.—Kingston: December 31, 1946, and February 5 and 7, 1947, 3 females collected; December 3, 1946, through February 7, 1947, 9 birds observed (Tordoff, 1952, p. 321). Port Royal Mountain: February 18, 1879, specimen collected by E. Newton (Merriam, 1885, p. 377).

St. Andrew Parish.—Hope: February 1879, specimen collected by E. Newton (Merriam, 1885, p. 377). Hermitage: April 8, 1879, specimen collected by E. Newton (Merriam, 1885, p. 377). Mt. Elizabeth: October 1 and 7, 1879, December 21, 1881, and March 16, 1882, specimens collected by E. Newton (Merriam 1885, p. 377).

Swan Islands

A specimen was collected on March 1, 1912 (Peters, 1913, p. 378). The Swan Islands are in the Caribbean Sea, between the Yucatan Peninsula and Jamaica, near latitude 18° N. and longitude 84° W.

² There are several records for the Bahama Islands that probably represent migrants, and they are treated as such here.

Mexico

Quintana Roo.—Santa Lucia: January 24, 1912, specimen collected (Peters, 1913, p. 378). Chetumal: February 12, 1949, specimen collected (Paynter, 1955, p. 242). Cozumel, Cozumel Island: December 27, 1961, specimen collected by L. C. Binford (Louisiana State University collection).

Campeche.—Pacaytain: January 15, 1940, specimen collected (Traylor, 1941, p. 219).

Veracruz.—Veracruz: winter of 1887-88 (distribution files, Migratory Bird Populations Station).

British Honduras

February 20, 1956, specimen collected by S. M. Russell (Louisiana State University collection) in the Orange Walk District.

Migration

SPRING

Swainson's Warblers apparently follow the most direct routes in migrating from wintering to breeding grounds. From West Indian wintering grounds they apparently reach the United States by island-hopping to southern Florida. Birds moving northward from eastern Cuba and Jamaica may touch some of the Bahama islands and cays enroute: there are March and April records from Bimini, Andros Island, and Cay Lobos.

The northern coast of Yucatan is a natural departure point for trans-Gulf flight to the Gulf Coast of the United States. Studies by G. H. Lowery (1945, p. 92-121; 1946, p. 175-211) and H. M. Stevenson (1957, p. 39-77) and observations by several other ornithologists lend credence to a trans-Gulf movement of Swainson's Warblers from the northern coast of Yucatan and the shore of the Bay of Campeche. The distribution of casualties at the base of the Tall Timbers TV tower near Tallahassee, Fla., 50 miles from the Gulf, indicates that the spring flight through that region is mainly in a southwest-to-northeast direction (Stoddard and Norris, 1967, p. 11, 15). Stoddard and Norris believe that this is mainly a trans-Gulf flight, with a minor segment of the flight skirting the Gulf. The lesser migration, which they refer to as the "Florida Peninsula-West Indian Flight" comes through mainly on easterly, southeasterly, and southerly winds.

It is probable that some of the Swainson's Warblers that winter in eastern Mexico migrate around the Gulf, moving northward along the eastern coasts of Mexico and Texas. The numerous spring records from coastal Texas could represent both trans-Gulf and circum-Gulf migrants.

Exceptionally early arrivals reach Florida by the middle of or the third week of March. There are records by J. Johnson and D. R. Paulson for March 16 offshore near Eau Gallie and for March 19 at Goulds, south of Miami (Stevenson, 1960, p. 304), and Bush Key pond, Dry Tortugas, March 17, 1964 (Robertson and Mason, 1965, p. 136). The first wave of migrants reaches northern Florida during the last week in March. At Tallahassee, during the period 1956 to 1966, 14 of 83 birds striking the Tall

Timbers TV tower arrived in the last week of March (Stoddard and Norris, 1967, p. 71). The earliest arrival date at Tallahassee was March 21.

Earliest arrivals at other localities are as follows: New Orleans, La., one on March 30 and four on April 1 (Kopman, 1905, p. 292; and 1915, p. 186); Savannah, Ga., March 25 (Burleigh, 1958, p. 495); Macon, Ga., March 31 (B. Meanley, MS.); and noted by K. McCracken and E. Payne, Corpus Christi, Tex., March 28 (Webster, 1966, p. 531).

Average dates of first arrivals are: Baton Rouge, La., April 2 (Lowery, 1945, p. 107); Alexandria, La., April 3 (B. Meanley, MS.); Macon, Ga., April 3 (B. Meanley, MS.); Augusta, Ga., April 3 (J. F. Denton, Jr., personal communication); Suffolk, Va. (Dismal Swamp), April 15 (B. Meanley, MS.); Clayton, Ga. (mountains), April 17 (E. O. Mellinger, personal communication); Charleston, W. Va., April 15-17 (Sims and DeGarmo, 1948, p. 3); and Maryland-Delaware boundary (Pocomoke Swamp), April 21 (Meanley, 1950, p. 94).

The main flights at Tallahassee, Fla., for the period 1956 to 1966 were during the first and second weeks in April, when 50 of 83 birds that struck the Tall Timbers TV tower (Stoddard and Norris, 1967, p. 71) were reported to be this species. At Macon, Ga., from 1963 to 1968, the main flights were in the second week of April (B. Meanley, MS.). At Charleston, W. Va., the main flight was April 19 (Sims and DeGarmo, 1948, p. 3). At the Dismal Swamp in southeastern Virginia, the main flight was during the third week in April (B. Meanley, MS.).

FALL

During 3 years at Macon, Ga., and at Gillett, Ark., I made weekly observations from the time the local population arrived in the spring until it departed in the fall, and I found that most of the breeding population remained until about the middle of September. A. T. Wayne (1910, p. 150) reported that at Charleston, S.C., "The song period lasts from their arrival until September 15." E. Sims and W. R. DeGarmo (1948, p. 3) stated that at Charleston, W. Va., "singing males were heard briefly in early mornings as late as September 15."

Apparently the bulk of the birds migrate through the Deep South between the middle of September and the middle of October. At the Tall Timbers TV tower at Tallahassee, Fla., Stoddard and Norris (1967, p. 71) reported, 58 of 60 fall strikes of this species occurred between September 11 and October 10.

The earliest migrants reach the middle Gulf Coast by early

August and the Florida Keys by mid-August and early September. Migrants were reported at Gulfport, Miss., on August 8 and 19, and at Deer Island, Miss., on August 26 (Burleigh, 1945, p. 110); at Sombrero Key, Fla., on August 17 (Howell, 1932, p. 386); and at Dry Tortugas, Fla., by September 2-9 (Sprunt, 1951, p. 224).

Late records of departure are: Knoxville, Tenn., October 7 and 8 (Howell and Tanner, 1951, p. 62); Tybee Island, near Savannah, Ga., October 18 (distribution files, Migratory Bird Populations Station); Tallahassee, Fla., October 14 (Stoddard and Norris, 1967, p. 71); and Sombrero Key, Fla., November 8, 10, and 13 (Howell, 1932, p. 386).

The migration route to the wintering grounds is apparently the reverse of that to the breeding grounds. The distribution of casualties at the base of the Tall Timbers TV tower indicates that the heaviest flight is from northeast to southwest, the direction of trans-Gulf migration. Some birds that migrate through southern Florida also pass through the Tallahassee area in the fall (Stoddard and Norris, 1967, p. 71).

The coast of Georgia and the eastern coast of Florida are also a southward migration route, as evidenced by the following records: Tybee Island, Ga., September 23 and 24 and October 2 and 18 (Burleigh, 1958, p. 496); Jacksonville, Fla., October 5 and 7, 19 birds picked up at TV towers (Cunningham, 1965, p. 29); St. Augustine, Fla., September 14 (distribution files, Migratory Bird Populations Station); Miami, Fla., October 2 (L. A. Stimson, distribution files, Migratory Bird Populations Station); and Loxahatchee National Wildlife Refuge, Fla., October 6 (P. W. Sykes, Jr., personal communication).

Southward movement along the Gulf Coast in Texas and northern Mexico would be expected, but records are fewer for the fall than for the spring: Rockport, Tex., October 20 (C. H. Hagar, distribution files, Migratory Bird Populations Station); Kemak, Tex., September 27 (J. S. Heiser, distribution files, Migratory Bird Populations Station); and Matamoros, Tamaulipas, Mexico, just over the Texas border from Brownsville, August 29 (Phillips, 1911, p. 84).

Early arrival records in the West Indies are: Havana, Cuba, September 25 (Bent, 1953, p. 38); and Mt. Elizabeth, Jamaica, October 1 and 7 (Merriam, 1885, p. 377).

Ecological Relations

The optimum habitat of the Swainson's Warbler is a rich, damp (but not wet) woods with deep shade and moderately dense undergrowth. This combination occurs in the physiographic areas in which this species is nearly always found—namely, the floodplain and swamp forests of the Atlantic and Gulf Coastal Plains and certain plant associations of the mixed mesophytic forest of the Southern Appalachians. When in swamps, the Swainson's Warbler frequents those parts that usually are not inundated, but occasionally on the Coastal Plain it may be observed foraging along the wet margin of a swamp or in low wet spots that have been left from receding floodwaters in floodplain forests. In such situations, its foraging behavior on the ground may resemble that of the Louisiana Waterthrush (*Seiurus motacilla*). Where inundation is present in a floodplain forest, it is usually the result of late spring floods or heavy rains, after the birds have selected a breeding territory in a dry section of woods.

Whether on the Coastal Plain or in the mountains, this species is usually near some major drainage system. The river valleys provide moist conditions on the breeding grounds, as well as "highways" for migration.

In Coastal Plain forests, where most of my experience has been, it is my observation that the Swainson's Warbler, more than its closest avian associates, is restricted to the shadier part of the forest. Species such as the Carolina Wren (*Thryothorus ludovicianus*), the White-eyed Vireo (*Vireo griseus*), the Prothonotary Warbler (*Protonotaria citrea*), the Hooded Warbler (*Wilsonia citrina*), the Kentucky Warbler (*Oporornis formosus*), the Cardinal (*Richmondia cardinalis*), and the Rufous-sided Towhee (*Pipilo erythrophthalmus*) spend only a part of their time in parts of the forest as shady as those frequented most of the time by the Swainson's Warbler. The deep shade of the Swainson's Warbler environment is the result of dense upper canopy, layer of lower trees, and shrub strata. Herbaceous ground cover is absent in most of the warbler's habitats, and where it occurs it is usually of little consequence as a shade producer.

The Swainson's Warbler lives mostly in the shrub stratum and

on the ground. In many habitats, the shrub stratum, or undergrowth, is composed mainly of a single species such as giant cane in the floodplain forest, sweet pepperbush (*Clethra alnifolia*) in the swamp forest, scrub palmetto in the bottomland forest, and rhododendron (*Rhododendron maximum*) in the mixed mesophytic forest. The structure of the undergrowth may be remarkably uniform, as in some canebrakes, palmetto thickets, and sweet pepperbush stands.

COASTAL PLAIN

In the Coastal Plain Province, river floodplain forests and swamps are the principal physiographic types in which the Swainson's Warbler lives during the breeding season, or summer half of the year. Since the terms swamp, riverbottom, hardwood bottom, and floodplain forest are often used synonymously, an explanation of these terms seems appropriate. The lowland forest bordering a southern river is generally known to the forester or plant geographer as a riverbottom or bottomland. It is usually a complex of several forest communities, including swamps, floodplain forests (also known as hardwood bottoms), and riverfront hardwoods. Most swamps are permanently flooded except during droughts; they thus differ from floodplain forests which are periodically flooded, usually in late winter or spring. There are several types of swamps. Those in riverbottoms are known as river or alluvial swamps; they are found in the lowest part of the bottomland, either bordering the river or between the floodplain forest and adjacent uplands. Swamps found away from riverbottoms are known as nonalluvial or inland swamps; good examples are the Great Dismal and Okefenokee Swamps.

Recognized as subdivisions within the floodplain or bottomland forests of the lower Mississippi Valley are the first bottoms, and the ridge bottoms (or cane ridges). In low, poorly drained flats of the first bottoms, the Overcup Oak-Bitter Pecan (*Quercus lyrata*-*Carya aquatica*) type is predominant. The Sweetgum-Water Oak (*Liquidambar styraciflua*-*Quercus nigra*) type is found in the better drained parts of the first bottoms. Sweet Pecan (*Carya illinoensis*), Sweetgum, and Southern Red Oak (*Quercus falcata*) are prominent on the cane ridges. These subdivisions are not as distinct or are non-existent in the South Atlantic coastal floodplain forests.

In floodplain and swamp forests, the main plant formations selected by the warbler are usually canebrakes (figs. 9-12), scrub palmetto, and sweet pepperbush. Greenbrier (*Smilax* spp.) is



FIGURE 9.—Canebrake along the edge of the Ocmulgee River, about 3 miles south of Macon, Bibb County, Ga., 1968.

often associated with sweet pepperbush where the Swainson's Warbler is found.

The canebrake is the prime and classic habitat of the Swainson's Warbler on the Coastal Plain. This habitat has mostly disappeared, having been reclaimed for agriculture, or grazed, burned, or flooded out of existence. Canebrakes are restricted mostly to floodplain forests or hardwood bottoms. In the lower Mississippi River Valley they occur on first bottom ridges, which are well-drained areas; whereas on the South Atlantic Coastal Plain they occur along the river and stream edges in floodplain forests where there is little change in elevation from the river to the edge of the uplands. Thus, they are subject to partial inundation during periods when the bottomlands are flooded.

Scrub palmetto occurs in floodplain forests and swamps in the southern part of the Coastal Plain breeding range of the Swainson's Warbler. Sweet pepperbush is an important plant for the Swainson's Warbler in the northern part of its Atlantic Coastal Plain breeding range. This was the principal habitat in which I found it in the Great Dismal Swamp of southeastern Virginia and the Pocomoke Swamp on the Eastern Shore of Maryland. In some places, sweet pepperbush stalks have a somewhat canebrakelike aspect, the main stems growing fairly straight, with similar spacing or density and shade effect.



FIGURE 10.—Canebrake habitat in the Ocmulgee River floodplain forest near Macon, Ga. The longest poles are 30 feet in length. The diameter of the largest poles is $1\frac{1}{4}$ inches.



FIGURE 11.—Canebrake habitat in the Ocmulgee River floodplain forest near Macon, Ga. The overstory is mainly ash, hackberry, elm, and ash-leaved maple.



FIGURE 12.—Canebrake habitat in the Ocmulgee River floodplain forest near Macon, Ga. Of 91 territorial males that I observed along the Ocmulgee over a period of years, 87 had territories in canebrakes.

Ocmulgee River floodplain forest in Georgia

In this area the Swainson's Warbler is found in the extensive canebrakes some 3 to 5 miles southeast of Macon in Bibb County in central Georgia (Meanley, 1945). The largest stands I have ever seen of the fast-disappearing canebrake habitat occur in this area. In 1968, there were still some sections in the Ocmulgee



FIGURE 13.—Typical canebrake breeding territory occupied by a male Swainson's Warbler near Macon, Ga., May 1965.

floodplain forest where canebrakes, nearly uninterrupted, covered 1-square-mile areas. The cane poles in these stands averaged about 15 feet in height and three-fourths of an inch in diameter at ground level. The largest poles reached 30 feet in height and an inch and a half in diameter at base. In the *Living Bird*, Fifth Annual, (Meanley 1966, p. 155) I published notes on the density of a tract of cane in a male Swainson's Warbler territory (fig. 13) near Macon:

The number of cane poles in 10 quadrats varied from 18 to 75 per 10-foot-square quadrat. There were about 20,000 cane poles per acre in my sample area which was virtually devoid of other plants, except for a scattering of large trees.

Of 91 territorial males that I observed in seven nesting seasons near Macon, 87 had territories (averaging about 1 acre each) in patches of cane growing beneath the floodplain forest canopy. The floodplain forest in this area was composed mainly of the following trees (in descending order of abundance): hackberry (*Celtis occidentalis*), boxelder (*Acer Negundo*), red ash (*Fraxinus pennsylvanica*), American elm (*Ulmus americana*), sweetgum, water oak, swamp chestnut oak (*Quercus Michauxii*), silver maple (*Acer saccharinum*), and mulberry (*Morus* sp.). The understory was mostly cane, but in openings included blackberry (*Rubus* sp.), swamp privet (*Forestiera acuminata*), or saplings of the above-mentioned trees. The coverage of the combined strata of upper canopy, lower trees, and understory was about 85 percent. Twelve exposure meter readings, made at feeding sites of four Swainson's Warblers, ranged from 100 to 225 footcandles.

The ground in areas occupied by the warblers is dry except during periodic flooding. During three nesting seasons when I entered the floodplain forest the water was 6 feet deep in some canebrake areas where I usually conducted studies. Sometimes these floodwaters recede in less than a week, and the habitat returns to normal. Such flooding sometimes occurs during the height of the nesting season, with a devastating effect on nesting success, since the average nest height is about 4 feet, and some nests are only a foot and a half from the ground.

A 7-acre tract of cane about 3.5 miles southeast of Macon had three territorial males in 1944, five in 1945, four in 1963, and one in 1968. There was gradual reduction in the amount of cane in this tract over the 24-year period. In 1968, I counted 19 territorial males along a 2-mile transect about 5.5 miles southeast of Macon in an area known as Bond Swamp.

The following notes that I made on breeding bird associates appeared in the *Living Bird*, Fifth Annual, (Meanley 1966, p. 158-159):

In the Ocmulgee River floodplain forest near Macon, the nesting species in closest association with the Swainson's Warbler were the Cardinal (*Richmondia cardinalis*), Hooded Warbler (*Wilsonia citrina*), and the White-eyed Vireo (*Vireo griseus*). All three nested in or on the edge of canebrakes as well as in other plant associations. The Cardinal fed mainly along the edge of cane thickets and in forest openings such as logging roads. The Hooded Warbler, which fed regularly from 2 to 30 feet above the ground,

ranged through the more open growths of cane as well as the more open parts of the forest undergrowth. The White-eyed Vireo preferred mostly a less homogeneous habitat, more often the edge of viney thickets, and usually fed from 5 to 20 feet above the ground.

Other species, present in canebrakes but not so closely associated with the Swainson's Warbler, were the Carolina Wren (*Thryothorus ludovicianus*), Kentucky Warbler (*Oporornis formosus*), Rufous-sided Towhee (*Pipilo erythrophthalmus*), and Prothonotary Warbler (*Protonotaria citrea*). The Carolina Wren ranged throughout the floodplain forest, especially about old logs and brush piles. The Kentucky Warbler occurred most often where there was a denser ground cover, particularly of herbaceous plants, than in the canebrakes. The Towhee, a ground-feeder like the Swainson's and Kentucky Warblers, fed in the canebrakes but usually where the leaf litter and cover was thicker than in the areas used by the Swainson's Warbler. The Towhee also fed in other parts of the forest and in the edge of habitats. The Prothonotary Warbler preferred the banks of streams that flowed through the canebrakes and the vegetation along the banks.

During migration, Worm-eating Warblers and Ovenbirds (*Seiurus aurocapillus*) moved through the canebrakes as well as other parts of the floodplain forest.

The Great Dismal Swamp

This extensive southern swamp a few miles south of Norfolk, Va., covers an area of about 600,000 acres in Nansemond and Norfolk Counties, Va., and in Pasquotank, Gates, and Camden Counties, N.C. In 1968 the Swamp was still a great wilderness, but with no virgin timber remaining. The part of the Swamp in which the Swainson's Warbler occurs is generally devoid of surface water (but low and damp) owing to drainage in connection with logging operations during the past 200 years. Being on low flat land with a high water table, some Swainson's Warbler territories are partially inundated after heavy rainfall.

The Dismal Swamp is quite diversified floristically but in the past apparently was predominantly forested with swamp blackgum (*Nyssa silvatica* var. *biflora*) (Kearney, 1901). It is in the remnant of this forest type, now of mixed species composition, that the Swainson's Warbler is mainly found today.

I examined such a mixed forest community along the northern end of Jericho Ditch (fig. 14), about 3 miles southeast of Suffolk, Va., in June 1966 and found that it was composed of the following plants: Predominant trees of the upper canopy were swamp blackgum, red maple (*Acer rubrum*), sweetgum, willow oak (*Quercus phellos*), water oak, tulip poplar (*Liriodendron Tulipifera*); lower trees were American holly (*Ilex opaca*), paw-paw (*Asimina triloba*), swamp magnolia (*Magnolia virginiana*), and red bay (*Persea borbonia*); undergrowth was mainly sweet pepperbush and greenbrier, but netted chain-fern (*Woodwardia areolata*)



FIGURE 14.—Mixed swamp hardwood habitat in the Dismal Swamp in southeastern Virginia, 1968. Major forest species are swamp blackgum, sweetgum, and red maple. Note Swainson's Warbler nest 2 feet from the ground in sweet pepperbush, center of picture.

covered the ground where there was more light. The Swainson's Warbler foraged mostly in openings between clumps of sweet pepperbush and greenbrier and in the small pure stands of sweet pepperbush. It nested mostly in the greenbrier tangles. A community of this composition also is the major Swainson's Warbler habitat in the Pocomoke Swamp on the Eastern Shore of Maryland.

I counted eight territorial males along a 0.5-mile transect in the vicinity of the Virginia-North Carolina line on April 20, 1958. Bird associates during the breeding season in the sweet pepperbush-greenbrier undergrowth are the White-eyed Vireo, Prothonotary Warbler, Prairie Warbler (*Dendroica discolor*), Ovenbird, Hooded Warbler, and Cardinal. The presence of the Prairie Warbler in this habitat was most unexpected, since nowhere else have I encountered it breeding in closed-forest habitat. An interesting breeding bird of this same swamp forest, but at higher elevations, is Wayne's Black-throated Green Warbler (*Dendroica virens waynei*).

Bayou Boeuf Swamp, La., and Monkey John Swamp, S.C.

Observations were made in the scrub palmetto breeding ground habitat in Bayou Boeuf Swamp near Alexandria, La., in the spring of 1956 and 1957, and in Monkey John Swamp near Savannah,



FIGURE 15.—Part of scrub palmetto territory of a male Swainson's Warbler in Monkey John Swamp, Jasper County, S.C., May 1964.

Ga., (fig. 15) in the spring of 1964. The physical features of these two areas were quite similar. Red ash, American elm, water oak, sweetgum, and hackberry formed an important part of the forest in both areas.

In Monkey John Swamp the density of the combined layers of the upper canopy and lower trees was about 90 percent. The undergrowth, almost entirely scrub palmetto, averaged about 3 feet in height, with about 800 plants per acre. Most of the ground area beneath the palmettos was dry. Wet spots under the palmettos in the territory of a Swainson's Warbler were generally avoided.

In the scrub palmetto habitat of Bayou Boeuf Swamp, I found a population density of 10 territorial males per 100 acres in April 1957.

Western Kentucky

R. M. Mengel (1965, p. 69) states that the ridge bottoms—the driest habitat of the alluvial forests, contain the finest broadleaf forest and the richest small bird populations of the region. It is in such areas that Swainson's Warbler is most numerous.

These are the cane ridges so favored by the Swainson's Warbler in the lower Mississippi Valley.

SOUTHERN APPALACHIANS

In the Southern Appalachians the Swainson's Warbler is primarily associated with the moist lower slopes of mountain ravines and various drainage systems of the Mixed Mesophytic Forest Region. On these lower slopes, where the proportion of hemlock in the mesic forest increases, rhododendron is often the main understory species; and it is within this association (figs. 16–17) that the warbler is most often found. It also occurs in some cove hardwood forests (fig. 18), where the understory may be composed of a heterogeneous growth of deciduous shrubs, and in other habitats.

In areas where the Swainson's Warbler is locally common, individuals of a population may "spill over" from optimum to marginal habitats, as cited by Brooks and Legg (1942, p. 70–80), who in West Virginia found a singing bird near the top of a ridge in a thicket beneath dead chestnut (*Castanea dentata*) trees. Parnell and Quay (1964, p. 139) reported a few Swainson's Warblers in dry sites, such as an oak-hickory forest in Toxaway Gorge in western North Carolina.

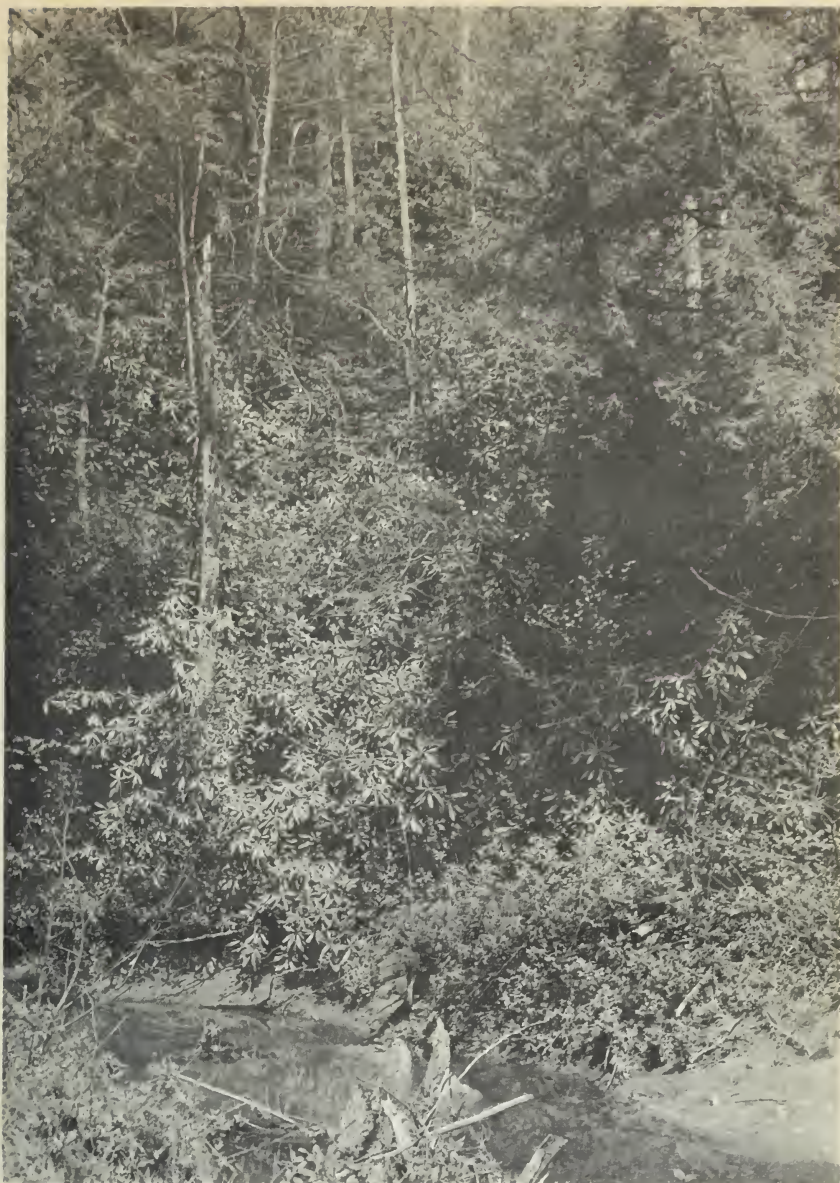


FIGURE 16.—*Rhododendron*-hemlock association. Mountain breeding habitat of the Swainson's Warbler along Collison Creek, on the Allegheny Plateau, Nicholas County, W. Va., May 15, 1966.



FIGURE 17.—Mountain breeding habitat, Collison Creek, Nicholas County, W. Va.



FIGURE 18.—Mature mountain cove hardwood habitat of the Swainson's Warbler near Charleston, Kanawha County, W. Va., May 1965. Tulip poplar is the dominant plant species.

Allegheny Plateau in West Virginia

In West Virginia the Swainson's Warbler is best known from the rugged Allegheny Plateau region of the south-central and southwestern part of the State. Studies of its habitats have been concentrated mainly in the Mt. Lookout section of Nicholas County along the Gauley River drainage (Brooks and Legg, 1942), and at Charleston in the Kanawha River area (Sims and DeGarmo, 1948).

In the Mt. Lookout region Brooks and Legg (1942, p. 78-79) found Swainson's Warblers in virtually all areas containing tangles of rhododendron, mountain laurel (*Kalmia latifolia*), hemlock, and American holly. In May 1940 they recorded 10 or 11 singing males within 1.5 miles along Franz Creek, a small branch of Collison Creek.

On the south side of the Kanawha River, in Donley Hollow, at the edge of the city of Charleston, Eleanor Sims found 18 Swainson's Warbler nests during 1945-47 (Sims and DeGarmo, 1948, p. 1). This is a rather good indication of the local abundance of the species in this section of the Allegheny Plateau.

At the foot of the mountain where Donley Hollow meets the floodplain the elevation is only 600 feet. As one travels up the



FIGURE 19.—Umbrella magnolia, prominent understory tree in habitat of the Swainson's Warbler near Charleston, W. Va.

ravine beside Donley Branch and climbs several hundred feet higher, Swainson's Warblers can be heard singing on both forested slopes, often two or three hundred feet up from Donley Branch. I counted seven singing males as I walked a mile up the hollow on May 15, 1965. There are probably fewer birds in the hollow now than at the time Sims and DeGarmo made their study, since the lower, moister slopes are now occupied by suburban residences.

The Donley Hollow habitat is like a Coastal Plain floodplain forest on the side of a hill. In these moist hollows or mountain ravines the dominant canopy species of the mature cove hardwoods forest is tulip poplar. The diameters at breast height of the four largest tulip poplars in one Swainson's Warbler breeding territory in 1965 were 25, 30, 33, and 36 inches. Other trees of the upper canopy layer were mainly beech (*Fagus grandifolia*), buckeye (*Aesculus* sp.), black oak (*Quercus velutina*), red maple, and sweetgum. Lower trees were umbrella magnolia (*Magnolia tripetala*) (fig. 19), dogwood (*Cornus florida*), and paw-paw. The undergrowth was mainly spicebush (*Lindera benzoin*), with occasional thickets of greenbrier and Japanese honeysuckle (*Lonicera japonica*). Thinly distributed herbaceous plants of the

ground flora were nettle (*Laportea canadensis*), mayapple (*Podophyllum peltatum*), violet (*Viola* sp.), baneberry (*Actaea* sp.), and Christmas fern (*Polystichum acrostichoides*). Twenty exposure meter readings at Swainson's Warbler feeding sites ranged from 50 to 245 footcandles.

The closest avian associates of the Swainson's Warbler in this habitat are the same as in most Coastal Plain breeding localities: the White-eyed Vireo, the Hooded and Kentucky Warblers, the Cardinal, and the Rufous-sided Towhee.

Toxaway River Gorge

Parnell and Quay (1964) found the Swainson's Warbler to be a common summer resident in Toxaway River Gorge, Transylvania County, N.C., in the summer of 1961. This section of southwestern North Carolina is in the part of the Southern Appalachians where North Carolina, South Carolina, and Georgia come together. There are breeding records from the mountains of all three States.

In Toxaway Gorge, Swainson's Warblers were found at altitudes of 1,200 to 2,800 feet. According to Parnell and Quay (1964, p. 144), these birds—

showed a preference for dense stands of rhododendron, mountain laurel, and dog hobble (*Leucothoe editorum*) along the narrow riverbottom Pine Flats. The Mixed Mesophytic Coves and Slopes and the Oak Forest were utilized to a lesser degree.

The Pine Flats are generally more mesic, more mature, and less disturbed than the other habitats. Canopy species are white pine (*Pinus strobus*), Virginia pine (*Pinus virginiana*), hemlock, and tulip poplar. The understory is mainly rhododendron. The Mixed Mesophytic Cove and Slope Forest canopies included such species as red maple, sweet birch (*Betula lenta*), hemlock, beech, basswood (*Tilia americana*), and tulip poplar. They have poorly developed shrub layers, but local thickets of rhododendron and laurel occur. The sparsity of Swainson's Warblers in this forest type may be due to the poorly developed shrub stratum. The Oak Forest gradually becomes differentiated from the Mixed Mesophytic type as the sites become drier. Mountain laurel is the main Oak Forest understory species.

Most of the same avian associates of the Swainson's Warbler as in the Coastal Plain and other localities of the Southern Appalachians are found in Toxaway Gorge. Parnell and Quay (1964, p. 145) list the Worm-eating Warbler (*Helmitheros vermivorus*) as an associate of the Swainson's Warbler. The Worm-eating War-

bler is also a nesting associate in the Pocomoke Swamp in Maryland, in the Arkansas River bottoms near Gillett, Ark., and at Charleston, W. Va., Mountain warblers breeding in the Toxaway Gorge included the Black-throated Blue (*Dendroica caerulescens*), the Black-throated Green (*Dendroica virens*), the Chestnut-sided (*Dendroica pensylvanica*), the Canada (*Wilsonia canadensis*), and the Blackburnian (*Dendroica fusca*).

Description

SIZE

The Swainson's Warbler is a rather short and stocky bird. Its length, 5 to 5½ inches, is about average for warblers, but it is heavier than most of the *Dendroica*s and *Vermivora*s. Four males collected during the breeding season weighed 13.2, 15.4, 16.2, and 16.6 grams (Mengel, 1965; Norris and Johnston, 1958; and L. C. Binford, Louisiana State University Collection). Two females taken in winter, one in Quintana Roo, Mexico, and one in British Honduras, weighed 13.7 and 13.9 grams (L. C. Binford and S. M. Russell, Louisiana State University Collection). A live male at Andros Island, Bahamas, in March, weighed 15.6 grams (Walkinshaw and Walkinshaw, 1961).

A series of birds that struck a Tallahassee, Fla., TV tower in spring migration averaged lighter than those striking the tower in the fall. The mean weight of the spring series of 15 birds was 14.9 grams, whereas the mean weight of the fall series of 19 was 18.9 grams (table 1). The Tallahassee TV tower is less than 50 miles from the Gulf Coast, and birds coming in from a trans-Gulf or circum-Gulf migration would have used up much of their reserve fat; whereas those leaving the United States would have a large fat reserve for the long journey to the wintering ground. Norris (1963, p. 47) reported that two birds that struck a TV tower in the Savannah River Valley in South Carolina on September 24, 1957, were excessively fat: one was recorded as having 19 percent fat, and the other, 24 percent.

TABLE 1.—*Weights of Swainson's Warblers killed at TV tower, Tallahassee, Fla., during migration*

[In grams]		
	Spring (15 specimens)	Fall (19 specimens)
Minimum	11.3	14.3
Maximum	15.7	20.4
Mean	14.9	18.9
Median	13.9	18.3
Standard deviation	±1.2	±1.7

Measurements in millimeters of 11 male specimens collected during the breeding season on the Coastal Plain are as follows: Wing,³ 67.5–72.5 (70.2); tail, 46.5–52.0 (49.1); exposed culmen, 15.0–16.5 (15.3); tarsus, 17.0–19.0 (17.8); middle toe, 12.5–14.0 (13.2). Measurements in millimeters of 10 female specimens collected during the breeding season on the Coastal Plains, are: Wing, 66.0–72.0 (69.0); tail, 46.5–52.0 (49.4); exposed culmen, 14.8–16.0 (15.3); tarsus, 17.5–19.0 (18.2); middle toe, 13.0–14.0 (13.3).

DISTINGUISHING CHARACTERS

Sexes of the Swainson's Warbler are alike. Upperparts, including wings, are brown, except the crown which is reddish brown; underparts are yellowish-white and unstreaked. There is no white in wings or tail. The bill is large, thick at the base, and sharply pointed.

Similar species.—The Worm-eating Warbler has black stripes on its crown. The Ovenbird is streaked below. Immature Connecticut Warblers (*Oporornis agilis*) and Mourning Warblers (*Oporornis philadelphia*) in fall plumage have eye rings.

ADULT PLUMAGE

The crown of the Swainson's Warbler varies from almost cinnamon to chocolate brown, with a barely distinct buffy median stripe from the base of the culmen through the forehead. There is a white or pale yellowish superciliary (eye) stripe, a dusky spot in front of the eye, and a brownish postocular streak. The sides of the head are otherwise pale buffy brownish. Back, scapulars, rump, upper tail coverts, tail, and wing coverts are olive brown or olive-grayish brown. Tertiaries are warmer brown (toward mummy or prouts brown); secondaries and primaries are dusky, edged with brown. (The closed wing appears browner than the back). Underparts are yellowish white to nearly plain white (possibly geographic variation), shaded with olive or olive-grayish on the sides. Adults in autumn are indistinguishable from breeding birds.

The bill is brownish, except the undersurface of the lower mandible, which is flesh colored. The iris is brown. Legs and feet are of a pale (pinkish) flesh color. The culmen is slightly curved, narrowed, and elevated between the nostrils. The foregoing description of plumage and soft parts is partly from R. Ridgway (1902 p. 436–437).

³ Wing measurements are for the chord, from bend of wing to tip of longest primary.

JUVENILE PLUMAGE

The juvenile wings and tail are similar to those of adults. Upperparts are brown; throat and chest are dark brown; and other underparts are mottled brown and white. There is no whitish line over the eye.

GEOGRAPHIC VARIATION

Breeding birds from the Southern Appalachians differ from Coastal Plain birds in that underparts tend to be whiter (less tinged with yellow). The underparts of 15 Coastal Plain specimens in breeding plumage were primrose yellow; whereas seven mountain specimens in breeding plumage were almost immaculate below but had a light suffusion of naphthalene yellow on breast and abdomen. There is no significant size difference between these two forms.

The mountain form was described as a new subspecies by B. Meanley and G. M. Bond (1950, p. 191-193) and is known as *Limnothlypis swainsonii alta* (Appalachian Swainson's Warbler). The type specimen, adult male, United States National Museum No. 362424, was collected at Walhalla, S.C., on June 25, 1940, by W. M. Perrygo and S. Y. Hoyt (original number 4,681).

MOLTING

Virtually nothing is known of the molt of this species. M. G. Vaiden (1940, p. 126) collected a male in partial molt on July 17, 1939, in Sunflower County, Miss.

Breeding Biology

TERRITORIAL BEHAVIOR

Arrival on the breeding grounds

The Swainson's Warbler is one of the last of the southern warblers to arrive on the breeding grounds, but it is earlier than most of the northern transient members of the family. When I visited the Dismal Swamp on April 11, 1969, all of the resident breeding warblers except the Swainson's Warbler had returned. Wayne's Black-throated Green Warbler had already begun to nest. Since the foliage was only about one-third out, and since Swainson's Warbler occupies the shadiest part of the swamp, its late appearance is probably timed with that of the foliage.

Since males sing the first day on the breeding grounds, the schedule of their arrival is better known than that of females; but females have struck the TV tower at Tall Timbers Research Station, Tallahassee, Fla., as early as the first week in April (William Dopson and James B. Cope, personal communication). At the Dismal Swamp in southeastern Virginia, earliest males have been recorded as arriving on April 15. On April 20, 1969, I observed a mated pair on their breeding territory in this swamp.

In the relatively late season of 1966, at my Macon, Ga., study area, the local male population arrived during a period of about 1 week. The first four males arrived on April 12; by the next morning there were eight males; there were nine on the 14th, and ten on the 15th, the date I departed from the area. When I returned on April 28 there were 19 males in the area. Apparently the males, and probably the females, arrive at night. I was on the breeding grounds 2 whole days preceding the arrival of the first males on the 12th, and on that morning I was there before dawn. At day-break on April 12, I heard the first Swainson's Warbler.

Homing

Individuals that establish a territory one year may return to the same place in succeeding years. John Weske banded a Swainson's Warbler on territory in the Pocomoke Swamp in Maryland in May 1960, and the bird was recovered at virtually the same place the following four seasons by mist-netters David Bridge and Vernon Kleen. In my study area in the Dismal Swamp, a marked male occupied the same general territory for 3 successive years.

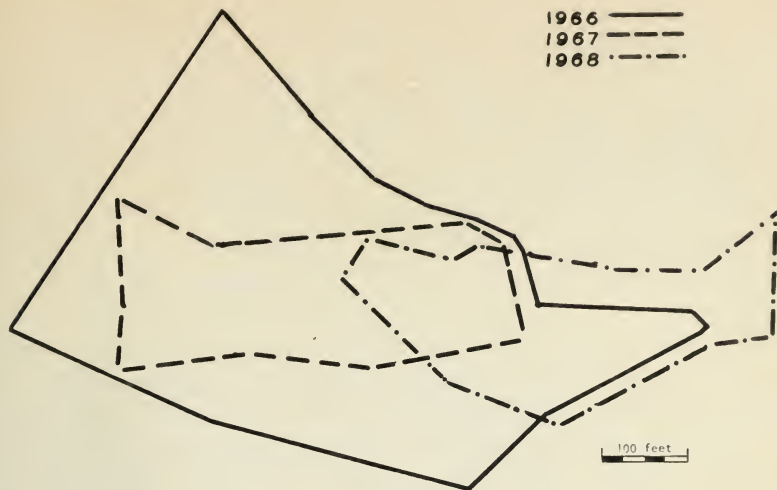


FIGURE 20.—Overlapping territories occupied by the same (marked) male Swainson's Warbler for three successive years (1966, 1967, 1968) in the Dismal Swamp in Virginia.

Territories

Males establish territories soon after arrival on their breeding grounds. The size and distribution of territories in an optimum area may depend upon the extent and arrangement of the habitat, as well as upon competition with other male Swainson's Warblers for food and space. Where prime habitat is limited in extent, it may support several territories, thus creating a group or "colony" of birds. This situation frequently occurs in southern canebrakes and is not unlike breeding "colonies" of the Kirtland's Warbler (*Dendroica kirtlandii*) in Michigan jack pine (*Pinus Banksiana*) habitat. In a 7-acre canebrake in the Ocmulgee River floodplain forest near Macon, Ga., there were four territories, and not all of the canebrake was occupied.

Sprunt and Denton (in Griscom and Sprunt, 1957 p. 51) reported that four territories in Georgia ranged in size from 0.72 to 0.91 acre (table 2). Two of the territories were adjacent and two were not. The smallest territory that I measured at Macon contained only 0.3 acre (table 2). It was in a block of woodland approximately 2 acres in size and was separated from the main forest by a cleared powerline right-of-way 50 yards wide.

In the Dismal Swamp, prime habitat is spotty; the territories are farther apart and larger than in the Ocmulgee River floodplain forest, where optimum habitat often occurs in larger blocks. The territory of one paired male in the Dismal Swamp covered

nearly 6 acres, and that of another nearly 4 acres (table 2). The overlapping territories occupied by the same Dismal Swamp male in 1966, 1967, and 1968 (fig. 20) contained 4.8, 1.7, and 1.6 acres respectively. In contrast, territories in the floodplain forest canebrakes seldom exceeded 1 acre. In two Dismal Swamp territories, only a part of each defended area was suitable for feeding and nesting; whereas in the canebrakes virtually all of the defended area was utilized for feeding. The "excess" area of the Dismal Swamp territories is used mainly for singing, but it is also defended.

Sometimes in discontinuous habitat a male may occupy a split territory or a territory composed of separate segments. One such territory in Monkey John Swamp, a few miles north of Savannah, Ga., had three segments. Two of the segments were on opposite sides of a cypress (*Taxodium distichum*) pond; the third was across a road from the pond. The occupied segments totaled 0.6 acre (table 2).

TABLE 2.—Size of Swainson's Warbler territories

Locality	Size (acres)	Reference
Ocmulgee River bottom, Bibb County, Ga.	0.3	Meanley, 1969, p. 247.
Monkey John Swamp, Jasper County, S.C.	0.6	Do.
Savannah River bottom, Richmond County, Ga.	0.72	Griscom and Sprunt, 1957, p. 51.
Do.....	0.79	Do.
Ocmulgee River bottom, Bibb County, Ga.	0.83	Do.
Little River Swamp, Tift County, Ga.	0.91	Do.
Dismal Swamp, Nansemond County, Va.	1.7	Meanley, 1969, p. 247.
Do.....	3.9	Do.
Do.....	4.8	Do.

Males may remain in the same area for most of the summer. One marked Arkansas male occupied the same territory for at least 4 months (April 15 to August 15). Six males occupied the same territories in my Dismal Swamp study area from April 20 to at least June 30, the date of my last visit that season.

However, shifting of boundaries takes place from time to time, and the size and shape of territories change. In the Dismal Swamp where Swainson's Warblers have plenty of room to spread out because of low population densities, and where territories are seldom contiguous, a territory may retain its identity throughout the breeding cycle.

During various phases of the breeding cycle different parts of the territory may receive major use, but the original territory

established by the male shortly after arrival on the breeding grounds may be defended at any time. When the male is not paired he uses most of the territory. If the first nest is destroyed, and the male and female become separated before the start of a second nesting attempt, the whole territory may be used. The part used is smallest during the mating and nest-building periods (fig. 21), and sometimes during egg-laying. Stenger and Falls

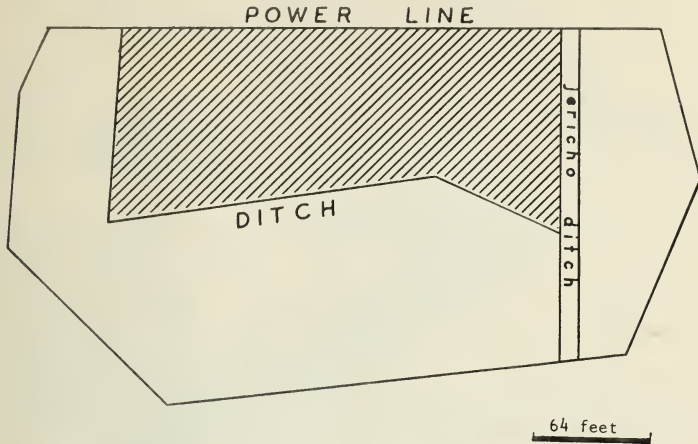


FIGURE 21.—Variation in size of the territory of a male Swainson's Warbler during breeding season. Only the hatched area (with densest cover) was occupied during the courtship and mating period. Dismal Swamp in Virginia, April 1969.

(1959, p. 136) found that the area utilized by Ovenbirds was larger during the premating, mating, incubation, and nesting periods than during nest-building and egg-laying.

Swainson's Warblers usually occupy larger territorial areas during the first few days after their arrival on the breeding grounds; and after the nesting season males that remain on their territories may extend the boundaries considerably. A male in the Dismal Swamp that occupied 4.1 acres in May and June occasionally extended his range over an 8-acre area in July.

The size and shape of a territory changes during each nesting attempt, because a different nest site is chosen each time and the sites may be several hundred feet apart. The male gives the nest site a wide berth when the female is incubating, thus giving the appearance that the nest is out of the territory when actually it is inside near the edge. The part of the territory most frequented by one Dismal Swamp male during a first nesting attempt was

avoided during the second nesting when the female built her nest there and started incubating.

Defense of territories

Territories are defended by singing, chasing, and combat. The song signals ownership, and each male's primary advertising song is usually different from his neighbor's.

Paired males appear to be more aggressive than unpaired males and usually initiate border encounters, which most often take place along territory boundaries. A paired and an unpaired male with adjacent territories at Macon, Ga., contended each time at virtually the same point along the boundary. As these males chased each other along the boundary, the paired female was close by but remained 10 to 15 feet within her territory, chipping excitedly.

A territorial male with an incubating mate at Pendleton Ferry, Ark., apparently had more time for hostile activity and thus was involved more often than the Macon paired male, which I observed during preincubation traveling with his mate. The Pendleton Ferry male would fly from any point in his territory deliberately to start a fight at the mutual boundary. He always began chipping excitedly as he moved toward his neighbor's territory, and both males chipped constantly during border clashes. In addition to chasing, the birds fluttered about on the ground after making contact and sometimes flew together a few feet up from the ground, grasping each other's bill.

Sometimes when a male invades a neighbor's territory and is chased out, he may perform a display on his side of the boundary. Such displays most often occur immediately after prolonged encounters. The wing and tail feathers are spread laterally (fig. 22), and the tail is vibrated. The bird sidesteps back and forth along a branch, frequently turning around, all the time chipping excitedly. Ficken and Ficken (1962, p. 110) observed a similar display in the Redstart (*Setophaga ruticilla*). At the end of a chase in which its adversary is evicted from the territory, a Swainson's Warbler male may fly up to a perch and sing vigorously for 10 to 15 seconds.

Following boundary encounters, males drift back into their territories and usually sing unbroken courses of songs for several minutes. Sometimes they start singing close to the boundary, in which case songs are incomplete, consisting only of the first two or three notes. Then as they move farther into their respective territories, they sing more complete songs.



FIGURE 22.—Display of a male Swainson's Warbler during or immediately following a boundary dispute with a neighboring male. The display resembles a female soliciting copulation. The wings are quivered, the tail feathers are alternately spread and closed, and the bird may step sideways back and forth along the limb.

There is usually little antagonism toward other species, and vice versa. White-eyed Vireos, Prothonotary Warblers, Hooded Warblers, Cardinals, and occasionally other species nest in territories of the Swainson's Warbler and, like the Swainson's Warbler, live close to the ground. On one occasion I saw a Hooded Warbler chase a Swainson's Warbler, after which the latter flew to a high branch within its territory and sang vigorously for about 10 seconds.

COURTSHIP AND MATING

I have never been present the minute the pair-bond was formed, nor have I witnessed male courtship displays before pair formation.

On one occasion when a female entered a male's territory for what I believe was the first time, she was chased for short dis-

tances but not driven beyond the territory boundary. The action of the two birds reminded me somewhat of the well-known sexual chase of Red-winged Blackbirds (*Agelaius phoeniceus*), when the females arrive on the breeding grounds.

During prenesting I observed a display by a paired male where he assumed a posture similar to a female ready for copulation. The posturing occurred when the male was perched about 3 feet from the ground and was approached by the female to within about 1 foot. When the female alighted near the male, he uttered a faint *twee-twee-twee* that was barely audible from where I was standing less than 8 feet away. The next day under similar circumstances, the same male extended his rump feathers only and uttered the same faint notes.

Also during prenesting, a paired male was observed to perform a "moth" or floating" flight. I could not locate the female at the time.

Vocalizations

During the courtship and mating period, a pair spends most of the day foraging on the ground, usually within 30 feet of each other and often only 2 to 3 feet apart. The male sings very little during this period and is otherwise less vociferous than the female. He may do some sustained singing early in the morning, usually before 7 a.m. I spent 3 consecutive days in the territory of one male, and after 7 a.m. on these days he sang four, none, and two primary advertising songs. During the day singing was more subdued and appeared to be for the purpose of signaling the female when she was momentarily out of contact with the male. Sometimes a song was incomplete, consisting only of the first, second, or third notes.

Vocalizations other than song are used by the pair to maintain contact. "Chipping" by the female is the most obvious and frequently used vocalization. Some females chip often enough for the investigator to follow a pair during most of the day in habitats where he can move about easily.

The chipping of the female often differs from the conventional alarm (chip) notes of both sexes. At times the chip note is more subdued, more of a squeak, and toward the end of the vocal performance the notes run together into a sort of muted chatter. At that point the chipping has the ring of excitement, and has attracted the male, who may attempt copulation.

Sometimes a very faint *chip* (that I could barely hear at 20 feet) is used by both members of the pair. This is a single chip,

well-spaced and not in a series like constant chipping when the birds seem excited. A paired female sometimes utters a faint *zeep* when a male in an adjacent territory sings.

On one occasion a pair that I had under observation was joined by a third bird, presumably a female. The visiting female fed with the pair for about 4 minutes, and at no time was chased by the male. The paired female chipped constantly while the interloper remained.

Pouncing

During the mating period males resort to pouncing on the females. The male flies to the female, who usually is foraging on the ground, and either pecks her rump feathers or pounces on her. I observed this behavior for several breeding seasons before I was sure that sometimes copulation was taking place. It was difficult to believe that copulation could occur under such circumstances. Hann (1937, p. 154) also had difficulty in observing copulation during similar behavior by Ovenbirds on the ground:

When copulation takes place on the ground, it is practically always accompanied by a struggle, which looks more like mortal combat than sexual intercourse. The fact that the female does not flee, and may even court the procedure, however, dispels any doubt as to her willingness. When they emerge from the struggle, the male usually flies to a nearby perch with an evident feeling of satisfaction, and the female, after shaking her ruffled feathers, proceeds with her eating or nest building.

Essentially the same behavior is exhibited by the Swainson's Warbler.

Pouncing may occur with or without an "invitation" from the female. Most of the time the female appears to be unaware that it is going to happen. Sometimes the female's excited chipping immediately preceeds the stalking and pouncing.

After observing pouncing behavior a few times, I could always anticipate when it was going to happen. The male, feeding on the ground, usually within 20 feet of his mate, discontinued feeding and mounted a branch or log, usually 6 to 12 inches from the ground. Then he remained virtually motionless in a crouched position for 1 to 5 minutes, facing and watching the female who was foraging on the ground or perhaps preening. In his crouched position the flank feathers of the male were slightly fluffed out, and his head was drawn in close to his body. Occasionally he would slowly move his head slightly to one side. When the female moved too far out of range, the male shifted to a closer perch and continued his crouched stance. His performance reminded me of a cat getting ready to pounce on its prey. He would then fly to

the female, and the two would flutter together on the ground. Sometimes the male stopped short of the female, and sometimes when contact was made copulation did not take place. The female sometimes responded with a faint *tweet-tweet-tweet*. Following such an encounter, the male might fly off singing a song as loud as the primary advertising song but not resembling it. These flights were sometimes upward in a sort of spiral. One male I watched often sang a whisper song after pouncing. Usually, however, the pair started feeding within a few feet of each other and near the spot where pouncing occurred. Pouncing is also known in the Red Warbler (*Ergaticus ruber*) (Elliott 1969, p. 188).

Nice (1943, p. 174-175) reported Song Sparrow (*Melospiza melodia*) pouncing as a form of courtship display "confined typically to the early stages of the nesting cycle." The male flies down to his mate, collides with her, and then flies away singing. Nice states that pouncing by the Song Sparrow early in the season has no immediate connection with copulation.

Pouncing on the mate occurs during the long period while song is inhibited and also during building. It may be a technique of the male for impressing himself upon his mate during the time of silence, of making his presence keenly felt.

Howard (1929, p. 22) observed that after the sexual chase recently paired Yellow Buntings (*Emberiza citrinella citrinella*) flutter together on or near the ground or peck each other as they rise in perpendicular flight, like fighting males. Howard believed that the sexual chase and pouncing show that the male is ready to copulate and that the female is not ready to receive him.

One male that I watched for 2 days pounced about three times each hour; another that I watched for 3 days before the beginning of nest building pounced about once every 10 minutes. A third male pounced about once an hour on the day nest building began; nest building was sporadic that day and occurred mostly in the morning, for just 2 or 3 minutes following pouncing.

Copulation occasionally occurs while the female is perched on a limb of a shrub or tree. When copulating in this manner the male sometimes holds onto the female's crown feathers.

NESTING BEHAVIOR

Nesting period

The prenesting period for paired Swainson's Warblers is relatively brief, for nesting begins soon after pair formation. For example, I visited the breeding grounds in the Dismal Swamp on April 12, 1969, at which time the Swainson's Warblers had not

yet returned. When I returned on April 20, I found birds paired in at least one territory, and by April 23, nest-building had started in that territory.

The earliest nesting anywhere is reported by Wayne (1910, p. 150) who collected eggs containing small embryos on April 28, at Charleston, S.C. However, May 1 is about the average date for the beginning of nesting throughout the Swainson's Warbler range.

Nest building at Macon, Ga., and Pendleton Ferry, Ark., started about 3 weeks after the first males arrived on the breeding grounds. A completed nest ready for eggs was found at Macon on April 27, 1946, and nests with full clutches were found by May 3, 1945. A nest containing one Swainson's Warbler egg and three Brown-headed Cowbird (*Molothrus ater*) eggs was found at Pendleton Ferry on May 1, 1967. This nest was probably constructed during the third week in April.

In the Dismal Swamp the earliest record of nest building is April 23, 1969. This is about 8 days after the average arrival date of first males. In this same area I observed two nests under construction on May 1.

On the Allegheny Plateau near Charleston, W. Va., Sims and DeGarmo (1948, p. 4) state, nest building begins about 2 weeks after arrival on the breeding grounds. They found a completed nest as early as May 1.

Renestings or second nestings occur throughout June and into early July. Perhaps the latest date is a nest with slightly incubated eggs found on July 13, 1886, at Savannah, Ga. (Perry 1886, p. 188). Young from this nest would have fledged about August 1.

Nest site and materials

For three or four days before nest building, and possibly longer, another activity of the pair is the examining of nest sites. The male of a pair that I watched at this activity led the way more than his mate, and at times he examined nest sites alone. One might therefore conclude that the male selects the nest site.

The average height of 10 nests in various localities was 4 feet 0 inches, with a range of 1 foot 9 inches to 6 feet 3 inches. Nests are usually built in the predominant understory vegetation (fig. 23). In the Dismal Swamp, nests are frequently placed in green-brier vines (fig. 24), as well as in Japanese honeysuckle, sweet pepperbush, and switch cane (*Arundinaria tecta*).

Most nests in my Dismal Swamp study area were located within 30 feet of a road or path. Vegetation in these situations is denser because of better exposure to light.



FIGURE 23.—A Swainson's Warbler incubating during flood stage in Ocmulgee River floodplain forest near Macon, Ga., May 1946. Water is 3 feet deep.

In Bayou Boeuf Swamp in central Louisiana, one nest in a scrub palmetto thicket was placed in a blackberry vine in such a way that it was directly beneath the broad frond of a scrub palmetto. The nest was completely shielded from above as if it had a roof over it 4 inches from the rim.

In a canebrake the nest is rarely located in the densest part of the stand, but is usually nearer the edge where the stand is thinner and the cane poles are smaller. In a mature mountain cove



FIGURE 24.—Swainson's Warbler nest in greenbrier vine, 2 feet above the ground, Dismal Swamp in Virginia.

hardwood forest at Charleston, W. Va., Sims and DeGarmo (1948, p. 4) found that—

the bird avoids placing the nest in dense cover, yet in all instances, a patch of some type of such cover is within a distance of twenty-five to fifty feet. In many cases, this thicket is a growth of greenbrier but may be grape, honeysuckle, blackberry or bittersweet. There appears to be a definite effort to locate the nest in such a manner that it is in close proximity to a screen of protective cover.

All nests that I found in territories of known boundaries were inside the territorial borders. However, they were often near the edge, or the male spent most of his time in an area to one side of the nest. Sprunt and Denton (in Griscom and Sprunt, 1957, p. 51) had this to say about the location of the nest in the defended territory:

The territory defended by the male is used primarily for mating and feeding and not for nesting. The nest itself is usually located along the margin of the territory but may be entirely outside of it . . .

I wonder whether Sprunt and Denton's observations were not made during the incubation period when most males avoid the nest site, which is often near the edge of the territory, thus giving the impression of being outside it. When the eggs hatch, the male attends the young along with the female; then the territory no longer has a buffer zone.

The Swainson's Warbler builds a large and bulky nest (fig. 25), apparently larger than that of other warblers that nest above the ground. Of two nests, in Dismal Swamp, that I saw under construction from the beginning, one took 2 days and one 3 days to complete, and they were built entirely by the females. At one site the male was often close by but visited the nest no more than twice each day during the 3 days of construction; the male did not assist in construction and apparently visited the nest in search of the female. At the other site, during the initial stages of construction the male occasionally accompanied the female to the nest as she flew in with nesting materials; he brought along no material and left almost immediately after arriving at the nest.

At both these Dismal Swamp nests the female did virtually all of the building before noon. Building of the nest that I watched



FIGURE 25.—The large, bulky nest of a Swainson's Warbler (right) and the nest of a nesting associate, the Cardinal, a species nearly twice the size of the warbler.

more closely took parts of 3 days, mostly between 7 and 11 a.m. Building was resumed in the late afternoon of each day between 4 and 5 p.m. However, during the late afternoon building period no more than half a dozen trips were made to the nest each day. The female made between 100 and 125 trips each morning. From 9:25 to 10 a.m. one morning, she made 34 trips, an average of about one trip a minute. During any sustained period she spent an average of 24 seconds at the nest, with a range of 9 to 70 seconds. The female sometimes chipped a few times while working on the nest. During the nest-building period, her mate rarely sang after 8 a.m.

All nest materials were gathered from the ground within 30 feet of the nest. Dry leaves, used in the bulky part of the nest and the outer layer, were obtained from the drier part of the woods; the cypress needles and red maple flower pedicels used in the lining came from a wet spot near the nest site.

Nests are constructed of a rather wide assortment of materials, but there is a selection of certain plant parts. The number of species of plants represented in a nest depends somewhat on the composition of the forest in which the nest is located. There seldom were more than a dozen species of plants in the nests I examined. The number of plant pieces in a Pendleton Ferry, Ark., nest totaled 418; there were 323 in a Dismal Swamp nest. The most pieces were in the lining of the cup. Sticks are seldom used in nests, and the few that occur seem almost incidental. But the first of three nests built by a female in a single season in the Dismal Swamp contained a great many sticks, which is the reason why it weighed more than the second and third nests.

In canebrakes the foundation of a nest is often a bunch of dead leaves that have lodged in the axils of a cane stalk. The Dismal Swamp female that built three nests used the relatively large leaves of the swamp magnolia as a platform for each of them. Each was at a site where several greenbrier vines crossed a horizontal limb of a shrub, so that the half dozen magnolia leaves formed a rather level base. Deposited upon these magnolia leaves were dried leaves, sticks, vines, and tendrils that formed the rather loose outer layer of the nest. Most of the leaves were swamp magnolia, red maple, red bay, and greenbrier. Most of the sticks were greenbrier.

The next layer was more compact, consisting almost entirely of decomposed or skeletonized leaves of the swamp magnolia. This layer formed the outer shell of a cup composed of finer materials in which the eggs were deposited. In positioning the

leaf skeletons, their tips were drawn toward the rim at a gradually sloping angle to the curve of the cup. All of them were placed in a regular pattern, being drawn clockwise from near the base on one side of the cup to emerge and protrude from the rim almost at the opposite side. All of the protruding petioles thus pointed away from the circle of the rim at a narrow angle. This layer was constructed similarly in all three nests. Swamp magnolia leaves, being elongated in shape, are well suited for this part of the nest structure.

Next to the layer of magnolia leaves was a layer of cypress twigs with needles. Cypress twigs and needles were also used as a lining for the upper inside half of the cup and for the rim of the nest. The lower inside half and bottom of the cup were lined mostly with pedicels of red maple flowers. All 11 of the Dismal Swamp nests were lined with these pedicels. Apparently they are a preferred item for the lining, since I have also found them in nests at Macon, Ga. F. M. Chapman (1907, p. 53) reports that J. N. Clark found them in linings of nests of the Worm-eating Warbler in New Jersey.

The Dismal Swamp female that built three nests in one season used fewer materials in constructing each succeeding nest; thus her nests were progressively lighter; dry weights were 47.7, 39.8, and 26.3 grams. Dimensions of an Arkansas nest were as follows: Greatest outside diameter, 15.0 cm.; inside diameter of cup, 4.0 by 5.0 cm.; outside depth, 7.8 cm.; inside depth, 4.2 cm.

EGG LAYING AND CLUTCH SIZE

At a Louisiana nest, there was a lapse of 2 days between the completion of the nest and the laying of the first egg; at a Dismal Swamp nest there was a lapse of 4 days. Eggs were laid daily until the clutches were complete, and incubation began with the laying of the last egg in each. At one Dismal Swamp nest the eggs were laid in the morning before 7 a.m. By marking eggs, incubation period at a nest at Augusta, Ga., was determined to be 14 or 15 days (J. Fred Denton, personal communication). The incubation period of eggs in a nest in the Dismal Swamp in 1969 was 13 days (F. C. Burford, personal communication). The first egg of this clutch of four was laid on May 1, and an egg was deposited daily; the first egg was hatching at 6:30 a.m. on May 17.

Of six first clutches in nests in Georgia, four consisted of three eggs each and two had four eggs. Of second clutches in four nests

in Dismal Swamp, three had two eggs and one had three. The somewhat globular eggs are white (fig. 26), but slightly spotted eggs are found on rare occasions (Wayne 1910, p. 149).



FIGURE 26.—Nest and eggs of the Swainson's Warbler in cane.

Cowbird parasitism

In some parts of its breeding range the Swainson's Warbler may be rather heavily parasitized by the Brown-headed Cowbird. During the first week in May 1967 at Pendleton Ferry, Ark., I located three Swainson's Warbler nests, all of which were parasitized. At one of the nests the warbler was incubating three cowbird eggs and one of its own. Three days later it was still incubating, but one of the cowbird eggs and its own egg were missing. At another one of the nests a warbler was incubating a single cowbird egg, and at the third a warbler was incubating three cowbird eggs; evidently the warbler eggs had been removed by the cowbirds.

Kirn (1918, p. 97-98) reported several parasitized nests in Copan County, Okla.; Sims and DeGarmo (1948, p. 5), in the course of 3 years, found three of 18 nests parasitized at Charleston, W. Va. I found that none of 11 Dismal Swamp nests were parasitized. Dismal Swamp is near the northern limit of the southeastern breeding range hiatus of the cowbird (Webb and Wetherbee 1960, p. 83-87), and I found only two or three cowbirds during an entire day in the Swamp in the spring of 1968. From 1944 to 1946 at Macon, none of six nests were parasitized, since at that time the area was out of the cowbird breeding range. By 1960, however, cowbirds were commonly breeding there.

INCUBATION

Information on behavior during the incubation period was obtained from a nesting pair in the first week of May at Pendleton Ferry, Ark., and from a pair in the Dismal Swamp in the middle of June. The Pendleton Ferry pair was the one mentioned above whose nest contained three cowbird eggs and one warbler egg. The nest was located about 2 feet above the ground between two cane poles. The height of the Dismal Swamp nest was also about 2 feet, and it was placed in a greenbrier vine. At each nest, incubation was performed only by the female.

During incubation the Pendleton Ferry female spent about 78 percent of her daylight time on the nest. The average period on the nest was 70 minutes; the average period off was 19 minutes. The longest period on the nest was 110 minutes, and the shortest was 30 minutes. The longest period away from the nest was 25 minutes; the shortest was 15 minutes. The Dismal Swamp female averaged 54 minutes on and 15 minutes off the nest. Lawrence (1953, p. 138), summarizing studies of six wood warblers, found that the birds were at the nest 67 to 83 percent of the time.

The two females I observed always sat in the same positions when incubating. Each left the nest each time in the same direction and fed in the same general area. The Pendleton Ferry female fed as far as 75 yards from her nest, but usually only about 30 yards from it. She fed both alone and with her mate. On one occasion her mate, which had not sung for more than an hour, flew to within 50 feet of the nest and sang two songs. The female chipped and left the nest, and the two flew off together to feed. Sometimes on leaving the nest the female flew out to about 30 yards from the nest where she chipped several times, presumably to attract her mate.

Upon returning to the vicinity of her nest, each female invariably chipped two or three times just before settling down.

The Dismal Swamp female was often fed by her mate when she left the nest during the incubation period. She followed the male on the ground like a fledgling following its parent. The male, walking about with cocked tail, gathered food and presented it to her.

During the several days of my observations, the Pendleton Ferry male never visited the nest. He did not come closer than 40 feet and usually stayed more than 100 feet distant. The Dismal Swamp male once, while the female was off feeding, visited the nest briefly and, not finding the female there, flew off and began singing vigorously. At dusk the Pendleton Ferry male was usually seen closer to the nest (40 to 50 feet) than during the lighter part of the day. He fed and sang in all areas surrounding the nest but was seldom closer than 50 feet. He did not sing as much as an unmated male in an adjacent territory.

CARE OF NESTLINGS

Most of my information on the care of nestlings is based on observations made during a 7-hour period on July 7, 1967, in the Dismal Swamp. Between 9:45 a.m. and 4:45 p.m. the 3-day-old nestlings were fed 14 times, eight times by the male and six by the female. The intervals between feedings ranged from 9 to 59 minutes. The female was at the nest 53 percent of the time brooding the young and sometimes standing on the rim. If she was brooding when the male came to the nest, she moved to the rim while he fed the young. Only the male removed fecal sacs from this nest, although at a Macon, Ga., nest the female also removed fecal sacs, sometimes swallowing them.

The male always approached from the same direction and worked his way slowly through the undergrowth until he was 2

to 3 feet beneath the nest; then he hopped up to the rim. The female approached from various directions, and flew 20 to 30 feet directly to the rim of the nest. On three occasions the male and female departed from the nest at the same time. Each time they flew in different directions.

Sims and DeGarmo (1948, p. 5) found that at several West Virginia nests young left after 10 days of nest life. At Augusta, Ga., the young remained 12 or more days in their nests (Griscom and Sprunt 1957, p. 53). Young that I observed at Macon, Ga., fledged at 10 days.

CARE OF FLEDGLINGS

Fledglings of a Dismal Swamp brood, just 2 days out of the nest, were fed only by the female during my 2 days of observations (June 13-14, 1967). The male was usually within 100 feet of the young and sang much of the time. The three fledglings usually did not attempt to follow the parents; but stayed within a relatively small area where they waited for the female to return with food. Most of the time they were perched 6 to 12 inches from the ground in heavy cover. During one 2-hour period, two of the three fledglings remained close together (5 to 10 feet) within a 20-foot-square area; at other times they were 50 to 100 feet apart. Sometimes after being fed, a fledgling attempted to hop along after its parent, but was soon left behind as the parent flew off in quest of food.

The fledglings were fed an average of every 15 minutes. When returning with food the female would walk and hop, rather than fly, to the waiting young. The young, hearing the approaching female parent rustling through the leaf litter, would intensify their chipping as she reached a point about 20 feet from them.

On three occasions, just as the female was about to feed a fledgling, the male pounced on her. As related above, pouncing also occurs during the prenesting period after the birds have paired.

Voice

SONG

The song of the Swainson's Warbler is loud and ringing and of marked musical quality. As Dingle (in Bent, 1953, p. 36) states,

The bird student who hears the song of Swainson's warbler as he sings in his wooded retreat is fortunate, for it is one of the outstanding warbler songs and, once heard, leaves a lasting impression upon the listener. At a distance it bears much resemblance to the songs of the hooded warbler and

Louisiana waterthrush. Close up, however, the appealing quality, lacking in the other two, impresses the listener strongly.

Songs of different individuals of the species vary. I have stood in one spot and heard the songs of five Swainson's Warblers, each distinctly different.

The song consists of three or four high introductory notes, all separated, followed by a phrase of four or five syllables uttered rapidly and slurred (Brooks and Legg, 1942, p. 82).

The songs of seven birds were analyzed from tape recordings made by W. W. H. Gunn (in Griscom and Sprunt 1957, p. 26-27) at Charleston, W. Va. Gunn's rendition is as follows:

tee-o tee-o (tee) whit-sut-say bee-o, or *tee-o tee toot-sut-say bee-u*, or *whee-u whee whit-sut-say bee-o*.

... they have loud ringing songs closely resembling those of the Louisiana Waterthrush both in tonal quality and phraseology. However, certain characteristic differences are evident: First, songs of Swainson's Warblers are noticeably shorter in duration, being composed of fewer syllables. Then too, the slow opening notes comprising the first part of the song differ markedly in phrasing between the two species, and although there is a remarkable resemblance in the second portion of the song, the Louisiana Waterthrush then typically goes on to add a final phrase missing from songs of Swainson's Warblers.

Gunn says that the duration of the Swainson's song is $1\frac{1}{4}$ seconds and that of the Louisiana Waterthrush's $1\frac{1}{2}$ to 2 seconds.

At a distance the strongly accented slurred ending (the first note high in pitch, the second low) of the Hooded Warbler song is suggestive of the ending of the Swainson's Warbler song, and often is confusing.

Whisper song

Berger (1961, p. 169) defines the whisper song as "the soft inward rendering of the primary advertising song, with or without variations." Muted or whisper songs of the Swainson's Warbler are a continuous chatter or musical twittering that may go on for as long as 3 minutes. I have never noticed any resemblance to the primary advertising song; rather they sound more like the continuous chattering notes of Goldfinches (*Spinus tristis*) in the spring, but are more musical. I have also heard in the spring a chattering song of kinglets (*Regulus satrapa* and *R. calendula*) and Blue-gray Gnatcatchers (*Polioptila caerulea*) that sounded a bit like the Swainson's Warbler whisper song. In the floodplain forest canebrakes of the Ocmulgee River in Georgia in April, I have heard all four of these species rendering these notes at nearly the same time. There have been times when I was not sure

whether I was hearing a Swainson's Warbler whisper song or notes of the other three birds. In fact, the whisper songs of several species of warblers sound alike. I have been fooled by the Prothonotary Warbler and the Yellowthroat (*Geothlypis trichas*), thinking I was hearing a Swainson's Warbler.

The whisper song is seldom audible beyond 30 feet. It is given throughout the breeding season. Mayfield (1960, p. 127) thought that the Kirtland's Warbler sang whisper songs mainly when other males were nearby. Morse (1967, p. 497) found that in the Parula Warbler (*Parula americana*) muted and incomplete songs were associated with a high level of aggression. I have heard the Swainson's Warbler give the whisper song when in the presence of other males, following a conflict at a territorial border, when alone on an isolated territory, and after pouncing on a female just as she was about to feed fledglings. I have heard the whisper song of the Swainson's Warbler most often when there was no other male or female of the species, or any other bird, nearby.

The whisper song may be delivered when the bird is standing or moving on the ground, perched on a limb, or in flight. I heard one male give the whisper song as he flew along about 2 feet above the ground for a distance of 50 feet. The whisper and primary advertising songs may be alternated: I observed a perched Swainson's Warbler that sang both, preening in between, and then hopped to the ground, alternating the songs while foraging.

Flight song

I have heard flight songs that had no resemblance to whisper or primary advertising songs. They were as loud as the primary advertising songs but continuous and run together, and they lasted as long as the flight. One singing bird took off from the ground in a spiralling flight to a height of about 35 feet; another flew from the ground at a 60-degree angle to a perch 40 feet up.

Incomplete song

Incomplete songs—songs without endings and songs consisting of only the first, second, or third notes—may be heard at any time during the breeding season. As mentioned above, incomplete songs are sometimes given following territorial bouts with neighboring males. They are often heard when a bird is startled or frightened. For example, a Dismal Swamp male alternately sang only one and then two notes when a Common Grackle (*Quiscalus quiscula*), a nest robber, invaded his territory.

SINGING BEHAVIOR

The primary advertising song is sung only by the male, and so

are whisper songs, as far as I can ascertain. When singing the primary advertising song, the bird changes the position of its head more than that of its body. The body is only slightly angled upward from the silent perching position; the head is thrown back with the bill pointed upward at a sharp angle, although not quite perpendicular. (Bird artists who have attempted to portray a singing bird of this species have usually done so incorrectly.) The bird's head and body are not tilted upward when singing muted or whisper songs.

The Swainson's Warbler sings from the ground, and from trees, shrubs, vines, and logs, usually below 30 feet. I have heard a bird singing from a perch as high as 50 feet, but singing from such a height is very uncharacteristic.

Singing from the ground is usually sporadic, since it is done while hunting for food. The bird nearly always stops to sing when foraging along the ground, assuming virtually the same posture as when singing from a branch; sometimes it starts singing before coming to a complete halt. After a male has spent some time on the ground intermittently foraging and singing, he may fly to the limb of a tree, where he rests, preens, or continues singing.

During the first few days after they arrive on the breeding grounds, birds in the canebrakes of the Ocmulgee River floodplain forest sing much more often from the ground than from trees or shrubs. In 40 hours of observation, three of four individuals were observed to sing only from the ground during their first week, April 12-19, 1965. During April 12-15, 1966, soon after the birds had arrived on the breeding grounds, one male sang only from the ground when under observation for 10 hours. When I next observed this bird, on April 28, it sang also from trees. Another male sang 135 songs from the ground and 65 from trees when under observation for 90 minutes on April 15.

When the Swainson's Warbler sings from trees, some of the perches most often used are dead branches well out from the trunk in the lower parts of the trees. The bird sings from a stationary position when perched in a tree or shrub, as pointed out by Brewster (1885a, p. 73-74):

While singing he takes an easier posture, but rarely moves on his perch. If desirous of changing his position he flies from branch to branch instead of hopping through the twigs in the manner of most warblers.

However, a singing bird may reverse its position on the same perch and resume singing while faced in the opposite direction.

In the course of 1 hour a Charleston, W. Va., male sang from 18 perches, once only from each of 17, and five times from one.

In the Dismal Swamp on June 3, 1966, a Swainson's Warbler shifted from perch to perch during the first half hour or more of the morning song. The bird started singing at 4:27 a.m. It sang from the first location for 11 minutes, from the second for 10 minutes, from the third for 10 minutes, from the fourth for 4 minutes, from the fifth for 1 minute, and from the sixth for 1 minute. It began feeding and singing from the ground at 5:15 a.m.

Seasonal song cycle

The song period in the breeding range lasts from 5 to 6 months, depending on locality, but the most vigorous singing occurs during April and May. Males still mated in June and July sing almost as frequently as earlier in the breeding season. Singing is fairly regular but mostly in the morning until about August; it is sporadic from mid-August to mid-September when birds begin to leave the breeding grounds.

In floodplain forests of the Ocmulgee River in Georgia and the Arkansas River in Arkansas, I heard individuals singing daily in July and August. On August 6, 1966, during a 2-hour period (11 a.m. to 1 p.m.) when I was in a canebrake near Pendleton Ferry, Ark., a male sang 93 songs. In this same area on September 7, 1968, four males sang sporadically in the morning until about noon. They sang complete, incomplete, and whisper songs. Much of their singing was instigated by Carolina Wrens, which are among the loudest songsters of the southern woods.

The male sings vigorously following arrival on the breeding ground and until the pair bond is formed. Then, while traveling with and courting his mate during the prenesting period, he sings very little. Most of the singing is during the first 2 or 3 hours after daylight. After 7:30 or 8 a.m. during this period males may sing only half a dozen songs during the rest of the day. Such songs later in the day are usually for the purpose of rallying the mate.

During nest building, singing may be sporadic, and often very little singing is done. The male may sing infrequently in the morning while the female is working on the nest, but in the afternoon when nest building is at a virtual standstill the pair remains together and the male sings hardly at all. On the first day of nest building, a Dismal Swamp male sang only one cadence, of 7 seconds, between 9 a.m. and 6 p.m. The next day he did not sing at all after 9 a.m.

During incubation the male sings more often than during the courtship, mating, and nest-building periods. One of the functions

of song during incubation appears to be to let the female know of her mate's whereabouts. I assume this, since the incubating female, upon leaving the nest, often goes to the male, with whom she feeds.

Singing during the nestling period is sporadic, since the male assists in the feeding of the young; after the young leave the nest, apparently only the female attends them, and the male increases his singing. During a 2-hour period (10:30 a.m. to 12:30 p.m.) when a Dismal Swamp female was attending her fledglings, the male sang a course about once every 10 minutes. After destruction of its mate's first nest, another male sang vigorously throughout the day and moved about the territory much more than usual; the female became very quiet and avoided the male, although she remained in the territory.

Daily pattern

The daily singing schedules of the Swainson's Warbler and other passerine woodland birds are about the same. In the Ocmulgee River forest the first singing of the Swainson's Warbler and other woodland birds was noted on a mild, cloudy morning, April 14, 1966. Sunrise was at 6:07 a.m. The first bird that sang was a Cardinal at 5:25 a.m., followed by a Rufous-sided Towhee at 5:32, a White-throated Sparrow (*Zonotrichia albicollis*) at 5:33, a Wood Thrush (*Hylocichla mustelina*) at 5:35, and then two Swainson's Warblers at 5:47. The Swainson's was the first warbler to sing, followed by a Prothonotary Warbler at 5:55 a.m. and a Hooded Warbler at 5:57 a.m. Almost all species of woodland birds were singing by 6 a.m.

In one of my study areas in the Dismal Swamp on June 3, 1966, the first Swainson's Warbler sang at 4:27 a.m., following a Cardinal, Wood Thrush, Wood Pewee (*Contopus virens*), Crested Flycatcher (*Myiarchus crinitus*), Hooded Warbler, and Tufted Titmouse (*Parus bicolor*), all of which began singing after 4:05 a.m. Sunrise was at 4:44 a.m.

On April 14, 1966, in the Ocmulgee floodplain forest, two Swainson's Warblers with adjoining territories stopped singing at 7 and 7:14 p.m. On June 2, 1966, in the Dismal Swamp, a Swainson's Warbler sang until 6:45 p.m. Only the Wood Thrush, Cardinal, and Wood Pewee sang later in that section of the woods. Sunset was at about 7:28 p.m.

Rate of singing

A song is sung in a course or series, that is, a period of steady singing for several minutes at a time. Sometimes in the early

morning the pause between courses is so brief that they seem to run for half an hour or more. Norris and Hopkins (1947, p. 8) noted that the average interval between songs of a male at Tifton, Ga., was 10.7 seconds.

The rate of singing is usually faster at the beginning of a course of songs (see table 3). During the first hour of morning song on June 2, a Dismal Swamp male sang at a fast but gradually diminishing rate of speed: nine songs per minute for the first 8 minutes, and five or six per minute thereafter.

The rate of singing is sometimes relatively constant over long periods of time. A male in the Ocmulgee floodplain forest on April 19 sang between 40 and 46 songs (40, 42, 46, 43, 42) in each 15-minute period from 8 to 9:15 a.m. Table 4 shows songs per 15-minute interval by a male in the Dismal Swamp.

TABLE 3.—*Songs per minute in courses by a territorial male Swainson's Warbler*

[4:15 p.m. to 6:43 p.m., 15 June 1966, in the Dismal Swamp in Virginia. Data from Meanley, *Wilson Bulletin*, 1968, p. 75]

Minutes in course	Time	Songs in each minute
5.....	4:15-4:20	8, 5, 5, 3, 2.
5.....	4:27-4:32	8, 6, 5, 2, 4.
6.....	4:40-4:46	7, 7, 7, 4, 4, 4.
13.....	4:50-5:03	8, 6, 4, 5, 5, 4, 5, 6, 6, 5, 5, 4, 1.
12.....	5:13-5:25	9, 6, 5, 4, 5, 4, 4, 4, 3, 4, 4, 2.
5.....	5:26-5:31	5, 5, 5, 6, 5.
3.....	5:48-5:51	8, 4, 1.
2.....	6:14-6:16	5, 5.
5.....	6:33-6:38	7, 5, 3, 4, 2.
3.....	6:40-6:43	5, 6, 4.

TABLE 4.—*Number of songs per 15-minute interval of a territorial male Swainson's Warbler*

[Observation made 3 June 1966, at Dismal Swamp, Nansemond County, Va. Sunrise about 4:44 a.m., sunset about 7:28 p.m.; sunny most of day; first song at 4:27 a.m.; sang until 6:45 p.m. previous evening. Data from Meanley, Wilson Bulletin, 1968, p. 76]

Hour beginning at—	Songs in 15-minute period ending at —				Total songs in hour	Temperature in woods (° F.)
	15 min.	30 min.	45 min.	60 min.		
4 a.m.	0	27	84	75	186	42
5 a.m.	61	33	50	48	192	47
6 a.m.	52	51	44	47	194	51
7 a.m.	54	53	48	43	198	52
8 a.m.	38	47	35	35	155	59
9 a.m.	24	23	29	0	76	61
10 a.m.	0	0	0	0	0	67
11 a.m.	0	0	0	0	0	67
12 noon	0	0	0	0	0	69
1 p.m.	0	0	1	0	1	68
2 p.m.	0	25	7	3	35	70
3 p.m.	8	21	12	31	72	70
4 p.m.	21	1	20	17	59	69
5 p.m.	0	0	0	0	0	62
6 p.m.	0	0	0	0	0	60
7 p.m.	0	0	0	0	0	55
Total in day					1,168	

Cadence of delivery

As pointed out by Reynard (1963, p. 139), an additional feature of bird song "unconsciously recognized but not particularly noticed is the cadence of delivery." Reynard defined the cadence of delivery of a song as—

the average length of time from the first note of a song unit to the first note of the succeeding unit throughout the whole song performance. The period timed includes that in which the song unit is heard *and the silent period between song units.*

I recorded cadence of delivery of three territorial males on May 2 in the Dismal Swamp between 7 and 8 a.m.: the deliveries recorded were 20, 20, and 14. The average cadence for the sample was 13.7 seconds. Reynard (1963, p. 141-142) lists the cadence

of song delivery of several other parulids as follows: Yellow Warbler (*Dendroica petechia*), 11.2 seconds; Prairie Warbler, 12.9 seconds; Ovenbird, 21.2 seconds; and Hooded Warbler, 9.8 seconds.

Some of the factors that influence the rate of singing are the stage of the reproductive cycle, time of day, and degree of excitement. During the nest-building period one male Swainson's Warbler had an extremely rapid cadence of 4 seconds early in the morning (at 6, 6:30, and 6:35 a.m.). He was signaling his mate, which at the time was building the nest. The course, or series, was short in each case, containing only four to six songs. On each of the three occasions, the female discontinued nest building and flew to her mate, a distance of about 100 feet.

Comparison with associates

On hot June days in the Dismal Swamp, I found the Swainson's Warbler to be one of the most frequent singers in the woods if it had an active nest or fledged young in its territory. The Red-eyed Vireo (*Vireo olivaceus*) sang more continuously, but its song did not stand out like that of the Swainson's Warbler. In the early afternoon when song activity is generally at a minimum for most birds, the Swainson's Warbler often was the most persistent singer. On July 8, 1967, a Swainson's Warbler was the only species that I could hear singing during a driving rainstorm.

I have to disagree generally with Brewster (1885a, p. 72) who says that the Swainson's Warbler is a "fitful and uncertain singer" and that "you may wait for hours near his retreat, even in early morning, or late afternoon, without hearing a note." I have noted such behavior in many species of birds, but it may result from particular conditions at the time of observation. If one visits a Swainson's Warbler territory daily in the early part of the breeding season before pairing, it will soon be observed that this warbler sings as frequently as most of the other woodland birds. Frequency of singing, as pointed out above, depends on the stage of the breeding cycle, the time of day, and the meteorological conditions, among other factors. Between the formation of the pair bond and nesting, they sing very little.

ALARM OR CALL NOTE

Next to the primary advertising song, the *chip* or *tchip* note, given by both sexes, is the best known vocalization of the Swainson's Warbler. The *chip* note is sharper than the similar note of the Kentucky Warbler, an associate in much of the Swainson's Warbler breeding range. To me, the Swainson's Warbler *chip* is

most like the *chip* of the first or last note of the song of the White-eyed Vireo. The two species occur together in the Coastal Plain Province, and I often have been fooled by the Vireo. However, it is not long before the Vireo reveals its identity as it follows through with the rest of the song or starts singing after giving the sharp *chip* note. Brooks and Legg (1942, p. 83) thought the Swainson's Warbler *chip* similar to that of the Mourning Warbler.

The chip call is used during intraspecific territorial strife, when alarmed by such nest robbers as snakes, Blue Jays (*Cyanocitta cristata*), and Common Grackles, and as a call-note for members of a pair.

A variation of the chip note is used by the female during the mating period (see section on Courtship and Mating). In this case the notes may be softer and more musical, and they are run together, almost forming a chatterlike song.

Another vocalization uttered by both sexes resembles the *zeep* note of various species of warblers during fall migration. I have heard Swainson's Warbler give this note in September when still on the breeding territory. On April 28 in the Dismal Swamp, 3 days before nest building, I heard a female utter a soft *zeep* each time her mate sang. The note was so weak and the male so far from her that I am sure he seldom heard it.

Feeding Behavior and Food

FEEDING BEHAVIOR

The Swainson's Warbler is primarily a ground feeder, but it sometimes searches for food a few feet above the ground in undergrowth. It also forages along the top sides of logs that are lying on the ground, and it may fly to the side of a tree trunk to pick off an insect that is a foot or so from the ground. Sometimes it reaches or hops up a few inches from the ground to take insects from the undersides of leaves of low-growing herbaceous plants, and occasionally it flies from perches in the lower parts of trees in pursuit of insects. Large insects are held in the end of the bird's bill and beaten against the ground until broken into several pieces.

The Swainson's Warbler searches for food in a manner different from that of other ground-feeding parulids that I have observed. Insects are located mainly as the bird pokes its bill under leaves or piles of leaves, pushing them upward and searching the ground beneath or examining the undersides of the leaves. A leaf may be held up momentarily and tilted at an angle as the bird inspects the underside. If part of a leaf is curled, the upper and the lower mandible of the bird are parted to uncurl it. Sometimes, as the bird moves hurriedly forward lifting and shoving leaves from side to side, its entire body disappears beneath the leaves. Most of the Swainson's Warblers that I collected in the course of their food searching in the Ocmulgee River floodplain forest had their bills caked with mud.

The bill of the Swainson's Warbler is larger and sharper pointed than the bills of the Ovenbird, the Louisiana Waterthrush, and the Kentucky Warbler, ground-feeding parulids that in the generally level terrain of the southern floodplain forest obtain their food primarily from the surface of the leaf litter. The Kentucky Warbler works across the forest floor, often under a partial cover of low herbaceous vegetation such as wood-nettle, jewelweed (*Impatiens* sp.), or poison-ivy (*Rhus Toxicodendron*). It hops along, flushing insects and picking them off stems and from beneath leaves of low-growing plants, and pokes its bill into piles of leaves or sticks. The Ovenbird (a walker) feeds similarly, but more in the open, as does the Louisiana Waterthrush (also a

walker), which feeds about wet leaf litter and shallow pools and occasionally does some leaf-flipping, in contrast to the shoving aside and "plowing" of the leaf litter by the Swainson's Warbler. The Swainson's Warbler also obtains some food from the surface of the leaf litter.

Within a breeding territory, a male usually uses several, perhaps half a dozen, foraging areas on the ground to which it consistently returns. Such areas are usually less than 50 feet square and free of obstructions at and just above ground level. In one Georgia canebrake I observed a male for 30 minutes as it searched for food in one of these special feeding sites measuring 20 by 30 feet.

When foraging in the shrub strata or undergrowth, the Swainson's Warbler probes into clusters of dead leaves and the axils of cane plants, as is typical of the Worm-eating Warbler, a species which closely resembles the Swainson's Warbler in size and plumage and often occurs in the same place.

Bill wiping

After feeding, a Swainson's Warbler mounts a limb and, before preening, spends a number of seconds wiping its bill. Bill wiping presumably is done to remove caterpillar hairs or other insect parts and pieces of dirt. The Swainson's Warbler has a good reason to spend more time wiping its bill than most other parulids because of its continuous probing beneath the leaf mantle in moist or wet silty soil.

FOOD

A total of 11 Swainson's Warbler stomachs have been examined by biologists of the U. S. Department of the Interior. All were from birds collected in Alabama and Georgia canebrakes. These examinations indicate that the Swainson's Warbler is totally insectivorous. Among favorite food items typically occurring beneath the leaf mantle are crickets (Gryllidae), ground beetles (Carabidae), ants (Formicidae), and spiders (Arachnidae).

Caterpillars (Lepidoptera) occurred in five of six stomachs collected in May and June in Alabama and were the most important by volume in four; ground beetles were the principal food item in one; and hymenopterous insects (probably ants) were most important in one. Spiders occurred in three of the stomachs.

The following items, in order of volume, occurred in stomachs of two birds taken at Macon, Ga., in May: ground beetles, caterpillars, stinkbugs, (Pentatomidae), homopterous insects (Homoptera), silken fungus beetles (Nitidulidae), and beetle larvae.

Crickets formed 43 and 40 percent by volume of the stomach contents of two birds collected near Augusta, Ga., in September; other major items in the two stomachs were Acrydiinae (grasshoppers), ichneumids, ants, and spiders. A stomach taken at Augusta in August contained the following items: 13 insect or spider eggs and the mass of silky material covering them, 16 ants, two ground beetles, three unidentified beetles, seven undetermined insect larvae, one caterpillar, one millipede (Diplopida), one stinkbug, one rove beetle (Staphylinidae), one darkling beetle (Tenebrionidae), and one beetle larva.

Near Cienfuegos in Cuba, Eaton (1953, p. 172) collected several Swainson's Warbler stomachs that contained the bones of small lizards (Iguanidae). He also found such bones in the stomachs of Worm-eating Warblers and Ovenbirds.

Miscellaneous Notes on Behavior

GROUND LOCOMOTION

The gait of the Swainson's Warbler is different from that of any other ground-feeding parulid. In searching for food, usually in dry leaf litter, its gait is described by Brewster (1885a, p. 74) as "distinctly a walk." Norris (1963, p. 47) also observed that it walked, and that its "gait was rather rapid and jerky, suggestive of that of the starling." He further stated that the Swainson's Warbler may hop "when traversing leaf litter." After 25 years of observing this species for many hours each spring, I would say that it hops some of the time, though mostly it moves in a rather rapid step that is a sort of a cross between a walk and a hop, suggesting a canter.

In searching for food on the ground it moves along hurriedly, often turning from side to side, and sometimes making a complete turnabout (180°) in a single hop or jump.

Another characteristic peculiar to this species while foraging on the ground is the quivering or tremulous movement of the posterior part of its body which sometimes occurs. This is not just a tail movement, but a part of the lower trunk of the body also is involved. I have observed this movement in both sexes.

PREENING

"This species often sits and engages in preening and scratching—apparently more so than does any other warbler of my acquaintance." So writes Norris (1963, p. 47), a Georgia ornithologist who knows this warbler well. I once observed a male preening continuously for 7 minutes. They seem to do a lot of preening in the center of the breast; this behavior must be related to the method of foraging, wherein the breast constantly is coming in contact with leaves and soil.

HEAD SCRATCHING

Ficken and Ficken (1968, p. 136) have suggested that the "head scratching method may prove a valuable addition to the set of complex characters that can be used in defining genera." In the course of a series of observations of Swainson's Warblers in the Dismal Swamp in Virginia, I observed head scratching in

three individuals: four times in one, three times in another, and once in a third. The three birds used the direct method, bringing the foot forward and under the wing. Ficken and Ficken (1968, p. 136) indicate that some *Vermivora* scratch directly and others indirectly and that all species of *Dendroica* observed in the wild scratched indirectly.

TAIL SPREADING

Tail spreading or fanning by a male may occur following territorial boundary disputes with another male. This is usually done by a male that invades another's territory and is driven out. I once saw a male on territory fanning its tail while being pursued slowly by a Redstart that had young in the territory.

Factors Affecting the Population

The Swainson's Warbler is the least abundant of southern warblers, except for Bachman's Warbler. There are several reasons why the Swainson's Warbler is not more successful. From my observations it would appear that it has a lower nesting success than most other species of warblers. In a total of 16 nests of which I am reasonably sure that my presence had nothing to do with desertion, only three were successful. Some of these were second attempts; others were initial attempts, in which case the birds may have been successful on the second try. At three of the nests, cowbirds removed all of the Swainson's Warbler eggs. A mouse expropriated another nest during the laying period, and two nests were abandoned with clutches intact.

Some of the reasons for its low nesting success may be the vulnerability of the large, bulky nest that is poorly concealed, is located close to the ground, and contains white eggs. Other species of warblers nesting in the same breeding range have better-concealed nests, most of which are much smaller, and all of which contain speckled eggs except the very rare Bachman's Warbler, which also has white eggs. Furthermore, most Swainson's Warbler nests are lined with dark material, so that the white eggs stand out against the dark background.

In the Dismal Swamp, I found that whenever a Common Grackle or a Blue Jay had a nest in or near a Swainson's Warbler nesting territory, the warbler's nest was almost always robbed. However, since the Grackle and Jay begin nesting before the Swainson's Warbler, and their nesting seasons overlap the first nesting attempt of these warblers, a second attempt can be made after the two nest plunderers have completed nesting and left the area.

Since the Swainson's Warbler places its not-too-well-hidden nest close to the ground, it is well within the "cruising" range of various snakes and mammals. C. E. Collier, Jr., (1941, p. 28) discovered a milk snake (*Lampropeltis triangulum*) in the act of robbing a Swainson's Warbler nest, near Clarksville, Tenn. The snake had one of the warbler's eggs in its mouth at the time.

Cowbird parasitism is becoming a more important limiting factor. Friedmann (1929, p. 150) and Mayfield (1965, p. 13-18) believe that the cowbird originated in the prairies and plains of the West, and only in the last 100 years or so invaded the eastern forest. As late as 1950 most of the southeastern Coastal Plain

was outside the breeding range of the cowbird, but it is gradually extending its breeding range into that area (Webb and Wetherbee 1960, p. 83-87). The cowbird is a common breeding bird throughout the lower Mississippi Valley and Appalachian mountains nesting range of the Swainson's Warbler.

Since one of the choice nesting sites of the Swainson's Warbler in the Coastal Plain is the river floodplain forest, production is markedly limited when such areas become inundated during the nesting season. In the Ocmulgee River floodplain of central Georgia, virtually all of the Swainson's Warblers nest within half a mile of the river. This is where the canebrakes are located. Some of the birds nest right up to the river bank. I have seen some Swainson's Warbler territories that were under 12 feet of water. Three out of 10 years that I worked in this area the nesting ground was flooded during May when the Swainson's Warbler was nesting.

Calhoun (1941, p. 306) found a similar situation in the Hatchie River bottoms in Hardeman County, Tenn. He made the following statement about these conditions:

If the Swainson's warbler nests in this same type of region, it would be exceedingly difficult to study its nesting habits because such areas are subject to flooding in the spring and early summer.

In the Coastal Plain part of its range the Swainson's Warbler would probably have a difficult time maintaining its present population level, not only because of low nesting success, but also because of its narrow habitat requirements. Canebrakes, prime habitat of this species, have disappeared faster than any other bottomland plant community. Habitat has disappeared faster in the lower Mississippi Valley than elsewhere in the range. Very early, rich bottomlands of the lower Mississippi Valley were stripped of their valuable hardwood timber and then cleared and drained for the agricultural use of their highly productive soils. Habitat in the Great Dismal Swamp and some other South Atlantic lowlands has contracted because the deep shade required by this species disappeared with the harvesting of the mature forest. The cut-over areas were drained and reforested with pine.

It is possible that the Swainson's Warbler can adapt to so-called marginal Coastal Plain habitat better than is suspected. Some occur there, but these usually are bachelor males. But if the Swainson's Warbler ever has to make a last stand it may well be in the Southern Appalachians, where many of them occur in national forests and national parks or in areas unsuitable for agricultural production.

Summary

The Swainson's Warbler is one of the least known of southern birds. Studies of its life history and ecology were made by the author principally in canebrakes along the Ocmulgee River a few miles south of Macon, Ga., and near Pendleton Ferry, Ark., in deciduous thickets in the Dismal Swamp, Va., in scrub palmetto in Monkey John Swamp, S.C.; and in mountain cove hardwoods near Charleston, W. Va.

The Swainson's Warbler was described by Audubon from specimens collected by John Bachman on the banks of the Edisto River in South Carolina in 1832 or 1833. John Abbot, a Georgia naturalist, collected a specimen some 25 years earlier but made no record of the event. However, he made an identifiable portrait of the bird. His illustrations of birds were discovered many years later in several museums.

The Swainson's Warbler spends nearly 6 months in the United States. During this period (summer half of year) it is primarily associated with the river floodplain forests and swamps of the South Atlantic and Gulf Coastal Plain and the rich moist woods of the Mixed Mesophytic forest of the Southern Appalachians.

The main wintering ground is the Caribbean archipelago in the general latitude of 20° N., especially the islands of Jamaica and Cuba; individuals also winter in the Yucatan Peninsula and British Honduras.

Some migrants apparently fly across the Gulf, some around it. First spring migrants reach the southern coast of the United States usually by the last half of March or the first week in April. Most birds are on the breeding grounds by April 15, but some arrive by the first week in April. In the fall most have departed from the breeding grounds by September 15.

The optimum habitat is rich damp woods with deep shade, moderately dense undergrowth, and relatively dry ground. Giant cane, scrub palmetto, and sweet pepperbush are the most important plants of Coastal Plain breeding grounds; rhododendron and cove hardwood shrubs are important in the mountains.

In April 1968, I counted 19 territorial males along a 2-mile transect through canebrakes near Macon, Ga. I found eight territorial males along a 0.5-mile transect in the Dismal Swamp in

Virginia, April 20, 1958. Brooks and Legg counted 10 or 11 singing males along 1.5 miles of Franzzy Creek in Nicholas County, W. Va.

The Swainson's Warbler is 5 to 5½ inches in length, and during the breeding season weighs about 15 grams. Breeding birds of the Southern Appalachians usually have whiter underparts than Coastal Plains birds.

The Swainson's Warbler is one of the last of the southern warblers to arrive on the breeding grounds, but is earlier than most northern transient members of the family. One banded male returned to the same territory in Maryland for five consecutive breeding seasons.

Nine territories ranged in size from 0.3 to 4.8 acres. The size and shape of a territory varies during different phases of the breeding cycle.

Hostile encounters between neighboring males usually take place along territorial boundaries. Paired males usually initiate border encounters with unpaired males. A display is sometimes performed by an aggressive male after it is driven back into its territory.

During courtship and mating the male sings very little. Frequently he flies to the female, who usually is foraging on the ground, and either pecks at her rump or pounces on her. Copulation sometimes takes place during pouncing.

First nests usually are built by the first week in May. Although other investigators reported finding nests outside the defended territory, all nests that I found were within the territory. The large bulky nest of this species is usually placed 2 to 6 feet above the ground. It is built by the female from materials gathered close to the nest site; she takes 2 or 3 days to complete it.

Three and occasionally four white eggs are laid. At a Dismal Swamp nest the incubation period was 13 days. The cowbird parasitizes nests in some parts of the breeding range.

During incubation two females spent 54 and 78 percent of daylight time on the nest. Both sexes feed young and clean the nest. Young remain in the nest 10 to 12 days. Fledglings of one brood were attended only by the female.

The song of the Swainson's Warbler is loud and ringing and of marked musical quality. It consists of three or four high introductory notes, all separated, followed by a phrase of four or five syllables uttered rapidly, and slurred. Songs are delivered at a rate of about 8 or 9 per minute for the first few minutes of morning song, then decrease to 5 or 6 per minute for most of the

morning. Songs are given in courses or series. The rate of singing is usually faster at the beginning of a course. The number of songs sung by a territorial male in 1 day, June 3, in the Dismal Swamp was 1,168. It produced 186 songs the first hour and sang at a fairly constant rate from 5 to 8 a.m., 192, 194, and 198 songs per hour.

Muted or whisper songs are a continuous chatter that may go on for as long as 3 minutes. They do not resemble the primary advertising song and may be given in the presence of other Swainson's Warblers or when alone. The alarm note is a sharp *chip*. A weaker chip is used for communicating during courtship.

The primary advertising song is sung from the ground and from perches at low elevations. The whisper song is usually given from the ground.

The Swainson's Warbler is primarily a ground feeder, but sometimes searches for food a few feet above the ground in undergrowth. Insects, its main food, are located as the bird pokes its bill under leaves, pushing them upward and examining the underside, and searching the ground beneath. Foods gleaned from beneath the leaf mantle usually are ground beetles, crickets, ants, and spiders. Sometimes caterpillars are taken in the course of foraging in the shrub strata.

The usual gait of the Swainson's Warbler is a cross between a hop and a walk, suggesting a canter. The direct method is used in head scratching, that is, bringing the foot forward and under the wing. Tail spreading or fanning by a male may occur following a territorial boundary dispute with another male.

The Swainson's Warbler is one of the least abundant of southern warblers. It has a low nesting success because its large bulky nest is poorly concealed, is located close to the ground, and contains white eggs. In parts of its range it is highly parasitized by the cowbird. In some Coastal Plain floodplain forests, nests are destroyed during floods.

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